Comparative Ecology and Conservation of Rare Native Broom, *Carmichaelia* (Fabaceae), South Island, New Zealand

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Abbreviations

AK	Herbarium at the Auckland War Memorial Museum
CHR	Allan Herbarium, Landcare Research, Lincoln
DoC	Department of Conservation
E	East
GR	Grid reference, based on New Zealand National Grid (Geodetic Datum 1949) and New Zealand Topographical Map Series 260 (1 : 50 000)
N	North
RARE	Rare plant collection held at Allan Herbarium, Landcare Research, Lincoln
S	South
UoC	University of Canterbury, Christchurch, New Zealand
W	West
WELT	Herbarium at Te Papa, Wellington

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Abstract

Using a comparative approach, the presented study explores the ecology of ten species of native New Zealand broom, *Carmichaelia*, and their vulnerability to competition and herbivory, with the aim of gaining a better understanding of the significance of introduced species as a threat to rare indigenous plants in New Zealand. In particular, the study focuses on the relationship between characteristics of the *Carmichaelia* species and their vulnerability, as well as on other factors influencing the significance of introduced species as a threat.

To gain a better understanding of the ecology of the *Carmichaelia* species, their current habitats and associated plant communities were investigated using quantitative-descriptive methods in the field. The effect of competition with introduced plants was studied in two glasshouse experiments, differentiating above ground competition for light from below ground competition for nutrients and water. The experiments focussed on the early life-stage of seedling establishment of the *Carmichaelia* species. The impact of herbivory by introduced mammals was studied in four field-based exclosure trials, focussing on the effects on survival and reproductive activity of adult *Carmichaelia* plants.

The results showed that the effects of competition and herbivory vary between the different species. Furthermore, they provided a set of species characteristics that can be used as indicators to predict the vulnerability of *Carmichaelia* to the impact of introduced species. These indicators provide a useful tool for threatened species management, as they allow the identification of the most vulnerable species as well as the most significant threat to each species. Furthermore, the indicators can be used to group species, combining those with similar vulnerability profiles, and therefore, likely similar management needs.

However, the example of the *Carmichaelia* species also illustrated that the use of indicators for the vulnerability of threatened species is limited and needs to be combined with case-by-case studies to verify the actual significance of threats for each population of concern. The vulnerability profiles derived from species' characteristics can be used to guide such site-specific studies, ensuring they focus on the most relevant threat factors. This combination of the understanding of general patterns in the vulnerability of species with targeted species and site-specific studies will lead to increased efficiency in the conservation management of threatened plant species.

1 General Introduction

The successful conservation management of uncommon and seemingly, threatened species is of increasing importance in the face of a world wide dramatic decline of biodiversity. However, despite the urgency, appropriate techniques for the conservation of species are often still unclear. A thorough understanding of the processes that lead to decline and extinction in current environments is needed to enable the successful management of species at risk. Using a comparative approach, this study aims at contributing to this understanding by investigating the effects of introduced plants and animals on a group of indigenous New Zealand shrubs, the native New Zealand broom, *Carmichaelia*.

1.1 Background

Rarity of species can be regarded as a natural phenomenon. Every community contains species that can be described as rare, because they occur with very low abundance, and while some species are ubiquitous, occurring over wide geographic ranges, others have developed as rare local endemics (Gaston 1994; Kunin and Gaston 1997). The extinction of species also appears to be a natural process. It is documented in the fossil record for all eras in pre-historical times (May et al. 1995; Mace et al. 2001). Despite this, however, the currently observed decline in biodiversity is of concern, as the extinction rates calculated for the recent, historical period exceed by far the natural background rate estimated from the fossil record (May et al. 1995; Pimm et al. 1995). Moreover, current extinction rates appear to reach levels rivalling those found for pre-historic periods of mass extinctions, such as the events at the Cretaceous-Tertiary boundary (Ehrlich and Ehrlich 1981; Jablonski 1995). Over the last few decades, lists compiled to monitor the decline and the extinction of species have included increasing numbers of taxa. For example, while in 1990, 23 104 plant species were listed as threatened or extinct worldwide (World Conservation Monitoring Centre 1992), the number amounted to 33 798 in 1997, comprising 12.5% of the world's known vascular plants (World Conservation Monitoring Centre 1998). Although this increase may partly be due to the growing attention paid to rare taxa, the numbers clearly illustrate the magnitude of the problem.

The main difference between pre-historic and present extinction events lies in the factors responsible. While pre-historic extinctions were caused by abiotic processes and catastrophes, e.g., the impact of a large meteorite is thought to have led to the extinctions at the Cretaceous-Tertiary boundary (Charig 1989), extinctions today are the result of human

influence on the environment (Diamond 1989a, b; Simberloff 1998; Schlesinger et al. 2001). This fact hands the responsibility for the current decline in biodiversity, and all potential consequences, to humanity.

In the attempt to halt the ongoing decline of biodiversity, scientists have turned towards the study of rare species and the causes and underlying mechanisms of decline and extinction. The aim is to gain sufficient understanding of the processes involved to develop appropriate conservation management strategies. Regarding the management of already rare or threatened species, it is particularly important to understand precisely which factors pose threats to the species, as otherwise conservation efforts might be misdirected, and fail to achieve the intended outcome.

The example of the Californian condor (*Gymnogyps californianus*) illustrates this (Caughley 1994). The dramatic decline of this species in the last century was initially attributed to inadequacy of food supply, and feeding stations were set up to counteract this. Egg-shell thinning, which had been observed as a threat to predatory birds, was considered irrelevant for scavengers like the Californian condor. Later, when egg-shell thinning was nevertheless discovered to occur, the precise cause was never investigated, but was simply assumed to be linked to DDT. Therefore, the threat to the condor was assumed to be averted when DDT was banned in 1972. However, the population declined further, and in 1986, an egg laid by the last female to attempt breeding in the wild was found broken, showing the typical symptoms of egg-shell thinning. Analysis of tissue from condors found dead in the wild further revealed that they had died from lead poisoning, probably caused by ingesting bullet fragments from deer provided at the feeding stations. By then, it was too late, and the last condor was taken into captivity (Caughley 1994). If the management of this species had been based on proof rather than assumptions of causes, this outcome may have been avoided.

Case-by-Case Approach

The obvious and most frequently taken approach in identifying the precise causes for the decline of species is the detailed autecological study of the species of concern. This approach is based on the understanding that the causes of species decline and extinction are idiosyncratic, depending on the life history and ecological characteristics of each individual species (Given 1994; Simberloff 1998). Examples illustrate that the causal relationships are indeed complex. The extinction of *Trilepidea adamsii*, a New Zealand species of mistletoe, for instance, is believed to have been caused by habitat loss, over-collection, herbivory by introduced possums, the natural rarity of the species, its

specialisation to bird dispersal, environmental and demographic stochasticity, as well as by the interactions between all these factors (Norton 1995a). Lesica et al. (1995) identify a small ecological amplitude and lack of genetic variability, together with habitat destruction and environmental stochasticity as threats to *Howellia aquatilis*, a rare aquatic plant in the United States.

Given the multitude of factors and the likely complexity of their interactions, case studies appear as the only way of providing all the information necessary for the successful conservation management of threatened species. However, in the face of the current dramatic decline of biodiversity, and the usually limited resources available for conservation, this approach seems also not practicable and too slow. An increase in the efficiency of conservation efforts is necessary, based on more general directives applicable across a range of species. To achieve this, an understanding of the dynamics of threats, in particular, of the relationships between their effects and the characteristics of the affected species, seems essential (Simberloff 1998; Mace et al. 2001). The case-by-case approach limits precisely this understanding, because, while it acknowledges that effects vary with the life history and ecology of the species, case studies do not actually analyse the nature of these relationships. In response to this, scientists have taken a comparative approach, aiming at finding general patterns that clarify the causes for the decline and extinction of species.

The Study of Rarity

One comparative approach towards a better understanding of the mechanisms of decline and extinction is the study of rarity itself. Patterns in species characteristics associated with rarity are likely to provide insight into the causes and consequences of rarity, which in turn will increase our understanding of the processes leading to extinction (Gaston 1994). A difficulty in this approach arises from the fact that the group of species considered to be rare is very heterogeneous, as species can be rare for a variety of reasons, and their characteristics and responses to rarity vary accordingly. In the attempt to understand this heterogeneity, different types of rarity have been distinguished, based on variables such as range size, abundance, habitat specificity, history of distribution, and temporal persistence of the species (e.g., Rabinowitz et al. 1986; Fiedler and Ahouse 1992; Benayas et al. 1999). For current conservation purposes, the distinction between naturally and anthropogenically rare species seems of particular interest, as many species today are likely to be rare due to human impact (Fiedler and Ahouse 1992; de Lange and Norton 1998).

Numerous studies have investigated differences in species characteristics relating to the various types of rarity, often in comparison with common species, in an attempt to find

patterns that explain causes of rarity and the varying vulnerability of species to extinction (e.g., Hodgson 1986a, b; Mc Intyre 1996; Byers and Meagher 1997; Gillespie 1999; Hedge and Ellstrand 1999; Walck et al. 1999). However, so far, the results of these studies show little consistency, further emphasising the strong degree of heterogeneity within the group of rare species (Fiedler and Ahouse 1992; Kunin and Gaston 1997). However, the apparent lack of consistency could also be the result of a lack of consistency in methodology (Bevill and Louda 1999; Murray et al. 2002).

Patterns of Extinction

A second, comparative approach towards a better understanding of the causes of extinction focuses on patterns in the characteristics of extinction-prone species. Rates of local extinctions have been found to be particularly high for species with restricted geographic ranges or generally low abundance in their habitats, as well as for species with high natural population variability, poor dispersal ability, slow life history, or ecological specialisation (e.g., Terborgh and Winter 1980; Shaffer 1981; Pimm et al. 1988; Foufopoulos and Ives 1999; Purvis et al. 2000). Similar to the study of rarity, the detection of patterns in the characteristics of extinction-prone species is complicated by the strong heterogeneity within this group of species. Purvis et al. (2000), in a study analysing extinctions of carnivores and primates, found that only 50% of the total between-species variation could be explained by species characteristics, and attributed the rest of the variation to the effects of various anthropogenic factors as causes of extinction. The interpretation of patterns in the characteristics of extinction-prone species seems therefore limited.

The Concept of Minimum Viable Population Size

The concept of Minimum Viable population size (MVP) directly addresses the underlying mechanisms of species extinction by establishing a general model of the processes involved. It focuses on populations, as this is the unit usually dealt with in the conservation of threatened species. The probability of extinction for a given population increases with decreasing population size (Shaffer 1981; Pimm et al. 1988). The MVP has been derived from this relationship, defining the threshold size above which a population at a given locality is likely to persist with a certain probability over a set period of time (Shaffer 1981; Gilpin and Soulé 1986; Soulé 1987). Below this threshold the population is likely to become extinct, due to factors relating to density dependent characteristics of the species, random demographic and environmental variation, natural catastrophes, and genetic processes, such as inbreeding and genetic drift (Ziswiler 1967; Ehrenfeld 1970; Soulé 1980; Frankel and Soulé 1981; Shaffer 1981; Simberloff 1986). All these factors increase in significance with decreasing population size, and furthermore, are thought to interact in so-called ‘extinction

vortices', i.e. positive feed back loops that exacerbate the negative impact on the population (Gilpin and Soulé 1986).

Intrinsic and Extrinsic Factors

The factors driving the 'extinction vortices', i.e. species characteristics, stochastic events, catastrophes, and genetic processes, can be classified as intrinsic factors (Simberloff 1986; Caughley 1994; Lande 1998; Mace et al. 2001). They comprise natural ecological, demographic, and genetic phenomena, which threaten the persistence of species mainly when population sizes are below the MVP (Shaffer 1981; Gilpin and Soulé 1986; Lande 1998; Simberloff 1998). Distinguished from these are extrinsic factors, which comprise external, anthropogenic impacts, such as habitat loss, fragmentation, the impact of introduced species, and pollution (Simberloff 1986; Caughley 1994; Mace et al. 2001). These factors can further exacerbate the effect of the 'extinction vortices', but in contrast to intrinsic factors, the extrinsic factors also negatively affect larger populations that are well above the MVP.

The impact of extrinsic factors can lead to the decline of large populations down to levels at which they then become vulnerable to the impact of intrinsic factors. The latter can subsequently trigger the further decline and final extinction of the populations, but the intrinsic factors only represent the proximate causes of such extinctions. The ultimate cause lies in the extrinsic factors having set off the decline of the initially large population (Hedrick et al. 1996; Simberloff 1998; Mace et al. 2001). For example, habitat fragmentation is known to reduce the effective size of plant populations. It also limits pollinator movement between remaining habitat fragments. As a consequence, plant species with specialised pollination biology can suffer drastic reductions in seed set and seed viability after fragmentation, due to the lack of successful pollination (Jennersten 1995; Matsumura and Washitani 2000). While, in this case, the specialisation of the plant species and the reduction in pollinator availability function as the proximate causes of the species' extinction, the initial habitat fragmentation clearly represents the actual, ultimate cause. Extrinsic factors, caused by the direct and indirect effects of humans on the environment, have been identified as the ultimate drivers of most current species extinctions worldwide (Diamond 1989a; Given 1994; Pimm 1998; Simberloff 1998; Schlesinger et al. 2001).

If the conservation management of rare and threatened species is to be successful, both kinds of factors, intrinsic and extrinsic, as well as the interactions between them need to be fully understood (Caughley 1994; Hedrick et al. 1996; Asquith 2001; Mace et al. 2001). The consideration of intrinsic factors allows estimating the risk of extinction for populations below

or close to the MVP, and provides guidelines for the manipulation of small populations in conservation management (Gilpin and Soulé 1986; Pavlik 1994). However, if the aim is to establish self-sustaining populations, the effects of extrinsic factors need also to be fully understood and mitigated.

Population Viability Analysis

Population Viability Analysis (PVA) is one attempt in including both, intrinsic and extrinsic factors into the conservation of threatened species (Gilpin and Soulé 1986). These analyses model the viability of populations over time, taking into account the impact of potential threats, intrinsic and extrinsic (e.g., Menges 1990; Lesica 1995), as well as the impact of management practices (e.g., Pfab and Witkowski 2000). Through this, PVA allows estimating the significance of certain factors as threats, as well as the likely success of management strategies. However, successful PVA depends on the detailed knowledge of the autecology and life-history of the species of concern, as well as on extensive, and preferably long-term monitoring data (Shaffer 1990; Boyce 1992). As collecting these data is time and cost intensive, PVA have only been conducted for a limited number of species, limited in particular, in relation to plants. Similar to the case-by-case approach discussed earlier, this highlights again the need for more general directives in threatened species conservation. Management strategies are needed that are applicable across a range of species, based on an understanding of the effects of threat factors and their dynamics in relation to species characteristics.

Dynamics of Intrinsic Factors

Intrinsic factors and their dynamics are relatively well understood. Consistent with the traditional view of conservation biology as crisis discipline (Soulé 1985, 1986), they have received more attention in conservation research than extrinsic factors, as intrinsic factors seemed more significant for the extinction of populations immediately at risk (Caughley 1994; Simberloff 1998). Furthermore, the mechanisms underlying their effects have been intensively studied in other biological disciplines, such as genetics and population biology. The principles and mechanisms established in these research areas apply to the processes occurring in small populations, and thus explain the mechanisms of extinction (e.g., Soulé 1980; Goodman 1987; Lande 1993, 1998; Frankham 1995). In addition, although the precise effects might vary from species to species, they show patterns in relation to species characteristics, allowing predictions regarding the vulnerability of species towards intrinsic factors (Caughley 1994). For example, genetic stochasticity is more likely to pose a threat to iteroparous, long-lived species with small range sizes and poor dispersal than to short-lived

species with high reproductive rates and good dispersal ability. The opposite is true for the threat of demographic stochasticity (Gilpin and Soulé 1986).

Dynamics of Extrinsic Factors

Habitat loss, fragmentation, and the impact of introduced species have been identified as the main causes for the current decline of plant species worldwide (Diamond 1989a; Pimm 1998; Simberloff 1998; Schlesinger et al. 2001). However, in contrast to the intrinsic factors, the dynamics of these factors and their precise effects on threatened species are less well understood (Simberloff 1998; Mace et al. 2001). Mace et al. (2001) identify the study of the effects of extrinsic factors and their correlation with species characteristics as an area of high priority for research in conservation biology (see also Caughley 1994; Simberloff 1998).

The effects of habitat loss by complete destruction, of course, are easy to comprehend, and species of habitat types that are typically associated with areas of intensive human land use, are particularly vulnerable to this impact (Cropper 1993; Coates and Atkins 2001). For example, of the species currently considered to be highly threatened in New Zealand, approximately 30% are species of wetlands and lowland forest communities (Dopson et al. 1999), as these habitat types have been widely destroyed by land clearance and drainage for agriculture (c.f. Dugan 1993). However, habitat loss also occurs through gradual degradation, which is harder to identify, and whose effects are more difficult to predict than those of immediate destruction. It is often unclear what exactly constitutes suitable habitat for a particular threatened species, and which species are likely to be more adaptable to habitat change than others.

The effects of fragmentation are relatively well understood. Similar to the intrinsic factors, this impact has been more frequently studied, probably because fragmentation leads to and affects, in particular, small populations. Furthermore, in trying to understand the effects of fragmentation, conservation biologists can draw on theory developed in other areas of research, such as population biology and the theory of island biogeography (Diamond 1976; Wilcox 1980; Soulé 1986; Simberloff 1988). A number of studies have investigated patterns in the correlation of species characteristics to their vulnerability to fragmentation. These studies show that initial rarity, patchiness of distribution, high demographic variability, low intrinsic rates of population growth, poor dispersal ability, and specialisation are related to increased vulnerability of species to fragmentation (Karr 1991; Laurance 1991; Norton et al. 1995).

The general effects of introduced species on indigenous plants seem obvious: invasive plants compete for space and other resources, while introduced animals function as herbivores or agents of disease (Williamson 1996). However, the precise effects on individual species, and in particular, the factors determining the vulnerability of natives to the impact of introduced species are largely unclear.

Studies on competitive relationships between plants in general, have attempted to relate the competitive ability of species to their specific characteristics. Relative growth rate, maximum plant size, seed size, and numerous other traits have been mooted as possible correlates of competitive ability, but so far the results of these studies are controversial (Gaudet and Keddy 1988; Grace 1990; Goldberg 1996; Keddy 2001). Only few studies have directly addressed the factors determining the vulnerability of rare or threatened plants to competition (Groves 2002).

Regarding the impact of herbivory, Bilbrough and Richards (1993) found that the vulnerability of shrubs depended on their ability to activate buds and their resource allocation patterns. Mc Intyre (1996) found that plant architecture, in particular, the size and height of the rosettes of Asteraceae species influenced their vulnerability to herbivory by introduced mammals in Australia, while Wardle et al. (1998) describe relationships between the palatability of species and their ecophysiological characteristics.

Although the results of these studies so far may be inconsistent, they illustrate that a better understanding of the relationships between species' traits and their vulnerability to the impacts of introduced species could provide a useful tool in the conservation management of threatened species. It would allow predictions on the vulnerability of species based on their characteristics, and therefore, overcome the need for detailed case studies confirming the significance of threats. For example, the orchid *Pterostylis arenicola* and the low shrub *Pimelea spicata* are both negatively affected by the creeper *Asparagus asparagoides*, an invasive plant in Australia. Despite their very different growth forms, the vulnerability of both species was found to be the result of a strong overlap of their phenological cycle with that of the invader (Groves 2002). Other species with similar phenological cycles, therefore, are also likely to be negatively affected by *Asparagus asparagoides*.

Introduced Species as a Threat to Biodiversity in New Zealand

The effect of introduced species is rated as the key problem for indigenous taxa in many of the isolated regions of the world (Loope and Medeiros 1994; Godfray and Crawley 1998; Clout and Lowe 2000; Orians and Soulé 2001). Although invaders also pose a threat to

indigenous biodiversity in larger continents and more accessible regions, like the Americas or Europe (Pysek and Prach 1995; Vitousek et al. 1997; Rodriguez 2001), plants of isolated regions seem particularly vulnerable to this impact. As invasion is naturally a rare occurrence in isolated countries, indigenous species seem less adapted to competition with new arrivals. New Zealand is an example for such an isolated area. It represents one of the most isolated yet most invaded places on earth (Clout and Lowe 2000).

Accordingly, introduced species are believed to pose a major threat to indigenous biodiversity in New Zealand today (Williams 1997; Dopson et al. 1999; Williams and Timmins 2002). Competition with introduced plants has been repeatedly suggested as a cause of species decline in New Zealand, but the precise effects on threatened species and the factors determining their vulnerability have not been identified. Most studies focus on questions regarding the invasibility of communities and the characteristics of successful invaders (e.g., Duncan et al. 1997; Rose et al. 1998; Rose and Frampton 1999; Jesson et al. 2000), rather than the species under threat.

Similarly, most research on the effects of introduced mammalian herbivores in New Zealand has focussed on changes in structure and composition of vegetation at a community level (Veblen and Stewart 1980; Campbell 1990; Nugent et al. 2001). Only a small number of studies quantify the effects on individual species and the significance of herbivory as a threat to them (e.g., de Lange and Silbery 1993; Norton 2001).

1.2 Objective and Research Approach

To gain a better understanding of the impact of introduced species and their significance as threats to rare indigenous plants in New Zealand, this study investigated the effects of introduced plants and mammalian herbivores on a group of endemic New Zealand shrubs, the native broom, *Carmichaelia*. Using a comparative approach, the objective was to clarify patterns in the relationship between species' characteristics and their vulnerability to the threats imposed by introduced species. Furthermore, the relevance of such patterns to the practical management of threatened species was investigated.

Ten species within the genus of the New Zealand broom, *Carmichaelia*, were chosen as study species. Nine of these are currently listed as nationally rare or threatened (de Lange et al. 1999), and competition with introduced plants and herbivory by introduced mammals have repeatedly been suggested as major threats to their persistence (e.g., Purdie 1985; Buxton

1993; Heenan 1995, 1996a, b; Williams et al. 1996; Norton et al. 1998; Wardle 1999, 2000a, b; Grove 2001).

Carmichaelia species are phylogenetically very close, as the genus is monophyletic, and speciation has taken place relatively recently (Wagstaff et al. 1999). Despite this, the species differ substantially in their growth forms and other morphological traits, as well as in the habitats they occupy (Heenan 1995, 1996b, 1998a). Because of their phylogenetic proximity, these differences are likely to represent true adaptations caused by selective processes, rather than phylogenetic artefacts, and comparative studies can be interpreted accordingly (Harvey and Pagel 1991; Goldberg 1996).

The study presented here consisted of three main parts. First, the ecology of the various *Carmichaelia* species was investigated with respect to the characteristics of their current habitats and associated plant communities (chapter 4). This provided a better understanding of the habitat requirements of the species, as basis for the analysis of threats. The second part focused directly on the effects of introduced plants and mammalian herbivores. Competition with introduced plants was investigated in two glasshouse experiments, differentiating above ground competition for light from below ground competition for nutrients and water (chapter 5). The objective was to explore whether the vulnerability of the *Carmichaelia* species to competition correlated with their habitat ecology and other species characteristics. Herbivory by introduced mammals was studied in four field-based exclosure trials. The focus was on the precise effects of the herbivores on the plants, with the aim of assessing the significance of browse as a threat to the persistence of the populations (chapter 6). In the third part, the patterns that emerged in the competition and herbivory studies were applied to the *Carmichaelia* species to analyse their usefulness for the conservation management of threatened species (chapter 7).

To put the study into the context of the New Zealand environment, the thesis begins with a brief introduction to the natural history of New Zealand's South Island, which constituted the study area (chapter 2). The genus of the indigenous broom, *Carmichaelia*, and in particular, the ten study species will also be introduced (chapter 3).

2 Study Area

2.1 Geography

The South Island of New Zealand lies at mid-latitudes between 40° 30’ and 46° 40’ in the southern hemisphere. It is a long and narrow island, with its main axis stretching over almost 900 km from NE to SW, no place being further away from the coast than 130 km (Fig. 2.1). One of the main features of the island are the Southern Alps, a mountain range extending almost over the full length of the island and reaching altitudes of over 3700 m.

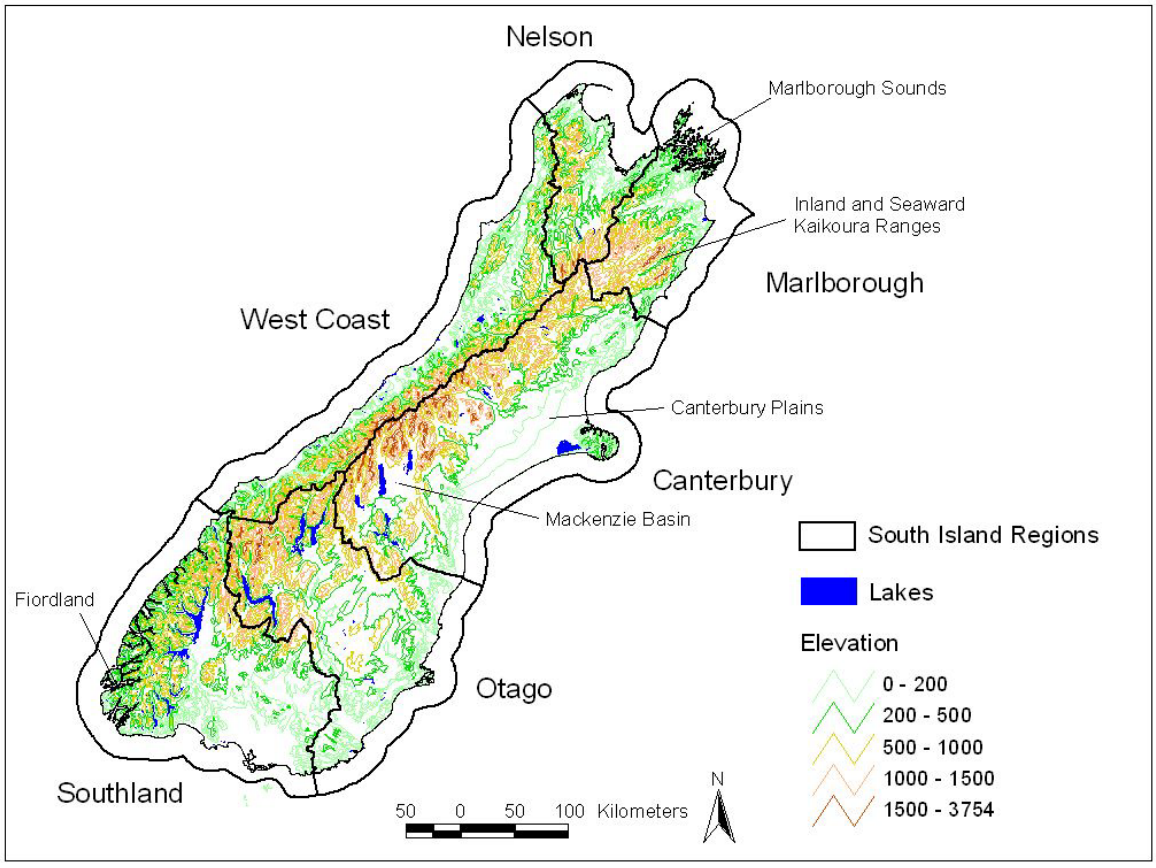


Fig. 2.1: The main regions of the South Island, New Zealand (boundaries based on Department of Conservation administrative boundaries).

The South Island has been divided into six administrative regions, the boundaries largely following natural features of the landscape. The Nelson and Marlborough regions comprise the far north of the island, latter region including the dissected landscape of the Marlborough Sounds, and the mountain ranges of the Inland and Seaward Kaikoura Ranges. Canterbury in the east, comprises the large area of the alluvial Canterbury Plains, stretching over 200 km from north to south with a maximum width of 50 km. The large intramontane Mackenzie

Basin is located in southern Canterbury. Otago's landscape represents an old peneplain dating back to the early Tertiary, that was again uplifted and broken up during the Kaikoura Orogeny 5-2 million years ago (Stevens 1980). It is characterised by long rounded ranges and wide open valleys. The West Coast region stretches in a narrow band along the western side of the Southern Alps, and Southland comprises the far south of the South Island with the Fiordland area to the west.

2.2 Geology and Geomorphology

Although some of its rocks are very old, dating back to the Precambrian (> 600 million years), New Zealand can be considered as geologically young, in the sense that its landmass has only recently been uplifted (Shaw 1960). The foundations of this landmass were formed, mainly as sediments, submerged at the outer edge of the supercontinent Gondwana, at least 200 million years ago. This supercontinent began to break up during the Cretaceous, and about 80 million years ago, the Tasman Sea began to form, isolating New Zealand from the other landmasses. As it moved slowly to its current position, the opening of an ocean gap between Antarctica and Australia lead to the establishment of the Circum-Antarctic Ocean Current and with it the West Wind Drift typical for latitudes between 40 and 60° S. Furthermore, as Antarctica moved towards the pole, developing a shield of permanent ice, the climate in the southern hemisphere cooled drastically (Shaw 1960; Stevens 1980; Thornton 1985).

The relief and landscapes characteristic of the South Island of New Zealand today have mainly been formed during the last 5 million years by three geomorphological processes: orogeny, glaciation, and erosion.

At least since the early Pliocene, 5 million years ago, New Zealand has been located at the collision zone of the Indian-Australian and the Pacific continental plates. The collision of these two plates and the resulting subduction of the Pacific Plate have led to orogenic processes uplifting the Southern Alps (Kaikoura Orogeny). This process is still continuing today, with active fault lines running along the western sides of the mountain ranges marking the boundary between the two continental plates (Shaw 1960; Stevens 1980).

Concurrent with the Kaikoura Orogeny, the climate cooled, leading to a series of alternating cold glacial and warmer interglacial periods during the Pleistocene (2 million – 10000 years ago). During the glacial periods, glaciers advanced from the mountains into lowland areas,

carving valleys and transporting huge masses of gravel and boulders to lower altitudes. During the interglacials, rivers carved their beds into the accumulated material leaving the surfaces to the side as distinct terraces which are characteristic of many valleys today. Other relics of the 'Ice Ages' are morainic hills and surfaces, as well as a number of large terminal lakes in inland Canterbury and Otago, and smaller kettlehole lakes along the western side of the southern alps (Shaw 1960; Stevens 1980).

The ongoing uplift of the mountain ranges has concurrently led to an increase in erosion. As the young mountain slopes are very steep, erosive forces are strong, and abundant material is transported downhill, mainly by water, channelled into streams. When the streams reach flatter terrain at the foot of the mountains, a large part of the transported material is deposited. This process has led to the formation of braided rivers and associated fans and terraces, with the Canterbury Plains representing the largest of these alluvial landforms in New Zealand (Shaw 1960).

2.3 Climate

The present climate of New Zealand has been classified as temperate, a climatic regime characterised by abundant rainfall and the absence of a cold winter period, at least at lower altitudes (Walter 1973). As New Zealand is surrounded by oceans, with the nearest larger landmass being 1600 km to the west, the climate also has a marked maritime influence. Weather patterns are determined by fronts and associated cyclones and anticyclones, developing through the interaction of converging subtropical and polar air masses. These systems migrate eastwards over the country, directed by the West Wind Drift (Sturman and Tapper 1996). As the Southern Alps of the South Island run more or less perpendicular to these westerly winds, they cause distinct regional differences in climatic conditions, in particular, between areas to the west and the east of the mountain ranges (Fig. 2.2).

The most striking difference relates to rainfall patterns, as areas to the west of the Southern Alps are subject to frequent orographic rainfalls, leading to totals in excess of 8000 mm/a in some areas. The east of the island, in contrast, lies in the rain shadow of the mountains with some inland areas in Otago and southern Canterbury experiencing semi-arid conditions with rainfall as low as 300 mm/a (Brenstrum 1999; New Zealand Meteorological Service 2002). Although annual rainfall averages are higher for the other eastern areas, most experience irregular periods of drought (Coulter 1966).

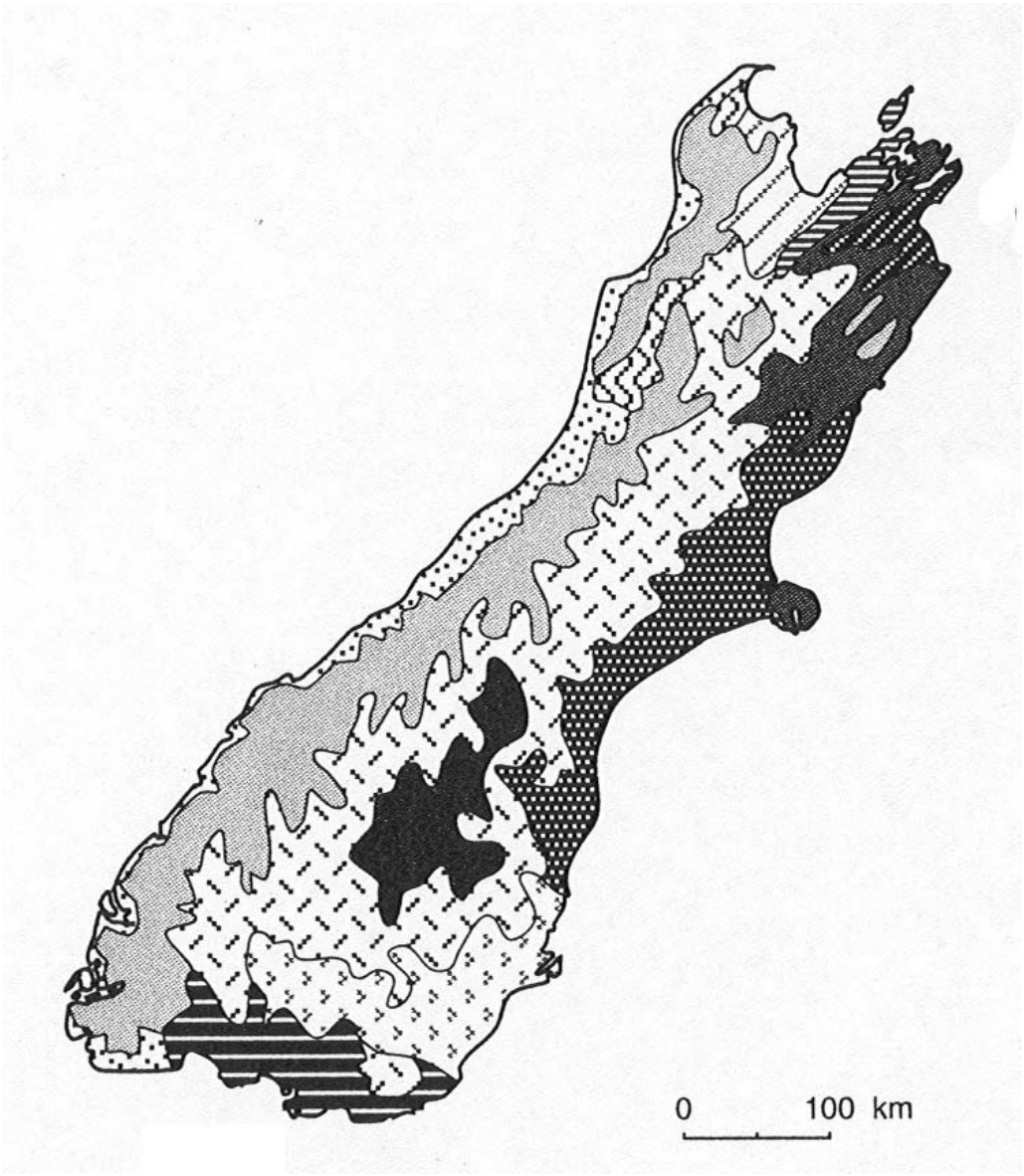


Fig. 2.2: Climatic regions of the South Island, New Zealand (altered after New Zealand Meteorological Service 1983).

As temperatures are largely a function of latitude and altitude, the annual temperature mean at sea level decreases from about 13°C in the north of the South Island to 10°C in the south, and temperatures drop by about 2°C with every 300 m increase in altitude (Meteorological Service of New Zealand 2002). However, a slight west-east contrast is also observable, with the daily as well as annual ranges being generally wider east of the Southern Alps. The semi-arid inland areas of Otago and southern Canterbury experience almost continental temperature conditions with relatively large daily and seasonal fluctuations.

A further characteristic feature of eastern areas are the föhn winds which develop as air is forced upwards over the ranges and then descends onto the eastern plains. These winds are hot and dry, and strongest and most frequent during spring.

2.4 Fauna and Flora

After the break-up of the Gondwana landmass, New Zealand's biota developed in relative isolation for 80 million years. Initially, the flora and fauna consisted only of elements inherited from the supercontinent, but were supplemented over time by a large number of migrants that made their way across the oceans (Mc Glone et al. 2001). These included amongst others the ancestors of the present *Coprosma, Hebe*, and *Carmichaelia* species (Bishop 1992). The majority of migrants came from Australia, aided by the West Wind Drift which established as the landmasses drifted apart (Stevens 1980).

When the first humans arrived, coming from Polynesia possibly as much as 2000 years ago (Holdaway 1999), New Zealand was largely a forested country (Atkinson and Cameron 1993). The fauna contained no terrestrial mammals except for two species of bat (King 1990), and was dominated by a large variety of birds, including a group of flightless ratites, the Moa (Dinornithiformes). The actual settlement of New Zealand is thought to have begun only in the late 13th century (Higham et al. 1999), when the Polynesians started to clear land for settlement and hunting. They burnt large tracts of forest, which was replaced by grassland and scrub (Mc Glone 1983). Total forest cover was reduced from an estimated 78% before human settlement to around 53% in 1800 AD (Atkinson and Cameron 1993). During the same time period, destruction of habitat and active hunting led to the decline and subsequent extinction of probably as much as 35 species of land bird (Atkinson and Cameron 1993), the most famous example being the Moa, which are thought to have become extinct within 160 years from the beginning of human settlement (Holdaway and Jacomb 2000). The Polynesians also introduced a number of species from their home

countries, such as sweet potatoes (taro (*Calocasia esculenta*) and kumara (*Ipomoea batatas*), Polynesian dogs (*Canis familiaris*) and kiore (*Rattus exulans*). Especially the latter, as the first ground-dwelling, omnivorous mammal to establish in New Zealand, is thought to have had a significant impact on New Zealand's indigenous biota (Atkinson and Möller 1990).

The first Europeans arrived in 1769, with extensive colonisation commencing in the early nineteenth century. The European settlers cleared more land reducing the forest cover to around 23% of the total land area (Atkinson and Cameron 1993). In addition, they began to farm the cleared areas, actively keeping them open with fire and grazing by livestock. Later, many areas were over-sown with exotic pasture grasses and fertilised to improve their quality as grazing country. Concurrently with the arrival of the Europeans began a massive wave of species introductions. Many were deliberate, like the introduction of farm animals and crop plants, but a large number of species also arrived accidentally as stowaways with the ships from Europe. Since the beginning of European settlement, 82 foreign species of mammals, birds and fish, and more than 2000 plant species have established with populations in the wild (Atkinson and Cameron 1993; Heenan et al. 1999). Today, these species form an integral part of New Zealand's natural systems.

The current state of New Zealand's indigenous biota stands in direct contrast to the drastic increase in introduced species. Ten species of land bird and seven plant species are known to have become extinct since 1800 (Atkinson and Cameron 1993; World Conservation Monitoring Centre 1998). and 511 plant taxa, equaling 22% of the indigenous vascular flora, are currently listed as uncommon or threatened (de Lange et al. 1999).

3 *Carmichaelia* Species - Native New Zealand Broom

The genus *Carmichaelia* (Fabaceae) comprises 24 species, 23 of which are endemic to New Zealand. The twenty-fourth species (*Carmichaelia exsul*) is restricted to Lord Howe Island in the Tasman Sea (Heenan 1998a).

3.1 General Description

Carmichaelia species are leafless woody plants. The group carries the common name of native New Zealand broom, as some of the species superficially resemble the European broom (*Cytisus scoparius*). However, the various species within the genus show a remarkable variety of growth forms. Some species are dwarf shrubs reaching only a few cm in height, while others grow into shrubs of 2-3 m, or even into small trees of 6-7 m (Fig. 3.1). Common to all *Carmichaelia* is the transformation of their shoots into cladodes, i.e. the shoots function as the main organs of photosynthetic activity, while leaves are reduced or entirely lacking.

A

B

Fig. 3.1: A - *C. stevensonii*, a tree species with a maximum height of 6 -7 m (Mt Alexander, Seaward Kaikoura Ranges); B - *C. vexillata*, one of the dwarf shrub species, reaching a maximum height of 15 cm (Pukaki-Ohau Canal, Mackenzie Basin).

Carmichaelia species are nitrogen-fixing plants forming symbiotic relationships with root-nodulating, acid-producing strains of *Rhizobium* (Wagstaff et al. 1999). As the New Zealand flora comprises only a few nitrogen-fixing species, *Carmichaelia* are likely to have fulfilled an important role in natural succession processes by colonising open and disturbed sites (Wardle 1991; Bellingham et al. 2001).

As members of the Fabaceae, *Carmichaelia* have the typical flowers of this family, consisting of a standard, wings, and keel (Fig. 3.2). They are mostly whitish in colour with purple marks, but some species flower pink (*C. carmichaeliae, C. glabrescens, C. torulosa*) or pale yellow (*C. williamsii*). *C. williamsii*, the only bird pollinated species in the genus, has the largest flowers, with their sepals reaching almost 3 cm in the length (Heenan and de Lange 1999). All other species are insect pollinated (native bees and flies, pers. obs.) and produce flowers of less than 1cm in length (Heenan 1995, 1996b). The flowers are usually arranged in racemes.

Fig. 3.2: Flowers of *C. kirkii*, Scrubby Creek, Benmore Range, southern Canterbury.

Most species flower in early summer, with flowering being restricted to a few weeks. However, some species show more extended periods of flowering, to the extreme that a few plants in a population can be found flowering at any time in the year (*C. curta*, *C. juncea*; pers. obs.). Other species, in contrast, do not flower every year, but in two-year cycles (*C. muritai* ; J. Clayton-Greene, DoC Renwick, pers. comm.; pers. obs.).

Carmichaelia seeds are spherical to kidney-shaped and range in size from 1-5 mm (maximum diameter). They develop in dry pods, and, as typical for many Fabaceae, the seeds of most *Carmichaelia* species have an impermeable testa effecting the physical dormancy of seeds (Grüner and Heenan 2001, see Appendix 6). Other forms of dormancy are not developed (Conner and Conner 1988; Williams et al. 1996; Grüner and Heenan

2001). The natural dormancy breaking processes are not understood, but Williams et al. (1996) showed that seeds of *C. muritai* can persist in the soil for as long as two years, suggesting the existence of soil seed banks. Also, in some species, seeds remain on the plants (*C. kirkii*, *C. australis*, *C. stevensonii*) or inside the unopened pods on the ground (*C. vexillata*, *C. astonii*) for at least one year, forming above ground seed banks (pers. obs.). As the seeds of most species show no adaptation to special dispersal mechanisms, they are likely to be mainly dispersed by gravity, probably aided by wind and water. *C. arborea* and *C. odorata* form an exception to the above description, as their seeds are flat with relatively thin testae, and wings that are likely to assist with wind distribution.

After germination, most *Carmichaelia* species exhibit heteroblasty of their shoots and/or leaves, i.e. they possess a distinct juvenile growth form, which is morphologically different from that of the adult plants. The transition between the two occurs in the first year after germination for all species (Heenan 1997a). The time period needed to reach maturity, in contrast, appears to vary considerably between the species. While some species have been observed to flower within the first (*C. juncea, C. curta*) or second year after germination (*C. kirkii, C. australis*; pers. obs.), *C. muritai* plants produce their first flowers only after ten years (J. Clayton-Greene, DoC Renwick, pers. comm.). All *Carmichaelia* seem to be relatively long-lived plants, as Heenan (1997b) counted 20 or more growth rings in stems of a range of species including shrub and tree species as well as dwarf shrubs.

Fourteen of the 23 New Zealand *Carmichaelia* species are currently listed as threatened or uncommon (de Lange et al. 1999). Most of these species are only known from a small number of populations or occur restricted to small areas, while others are still widespread, but believed to be declining (de Lange et al. 1999). Habitat loss or degradation due to anthropogenic or natural impacts, recruitment failure due to weed encroachment, browse and seed predation, over-collection, and inappropriate weed spraying have been identified as the main threats to the various species today (Dopson et al. 1999).

3.2 Evolution

The genus *Carmichaelia* is monophyletic, i.e. the present species have developed from one common ancestor (Heenan 1998b; Wagstaff et al. 1999). This ancestor is thought to have been a herbaceous plant which dispersed from Australia about 5 million years ago (Heenan 1998b; Wagstaff et al. 1999). Since then, the New Zealand descendants have adopted a woody growth form, and have radiated into the 23 species distinguished today. *Carmichaelia exsul* is believed to have developed after a more recent dispersal event from New Zealand to Lord Howe Island (Heenan 1998b; Wagstaff et al. 1999).

The radiation of the New Zealand *Carmichaelia* coincided with the uplift of the Southern Alps and with a general cooling of the climate, culminating in the 'Ice Ages' of the Pleistocene. Increased erosion and glaciation during this period led to the formation of new habitats, such as scree slopes, outwash fans, terrace complexes, and glacial moraines. The cooler climate and, in particular, the glaciation periods, were further associated with increasingly arid conditions. The strong adaptation of present *Carmichaelia* species to drought (Heenan 1997b) suggests that the genus radiated under these conditions, as drought-tolerance would have conferred a competitive advantage (Heenan 1998b; Wagstaff et al. 1999). In addition, as nitrogen-fixing plants, *Carmichaelia* were not dependent on fertile, established soils and could colonise the newly created and disturbed habitats. Speciation is likely to have been further enhanced by characteristics of the newly developed landscape itself, as its discontinuous alpine regions, which are separated by low passes and deep valleys, its sharp climatic gradients, and geological discontinuities provided for the necessary isolation of populations (Given 1981).

3.3 Study Species

Nine of the currently 14 threatened and uncommon *Carmichaelia* species were included in the research. They were chosen according to their growth forms to include dwarf shrubs, shrubs, and tree species, as well as one climber (Table 3.1). Furthermore, the species varied with respect to their habitats, as far as known prior to the study. *C. australis*, the most common *Carmichaelia* species, was also included to further widen the spectrum for the intended comparative approach.

Table 3.1: The ten study species, their current conservation status, growth forms, and habitats. Conservation status follows de Lange et al. (1999). Habitats are listed, as far as known prior to this study (S. Courtney, DoC Nelson, pers. comm.; see chapter 4 for a more detailed discussion of habitats).

Species	Conservation status	Growth form	Habitat
C. astonii	Range Restricted	Dwarf shrub	Rock outcrops
C. australis	Not listed, Common	Shrub	Various habitats
C. crassicaule	Gradual Decline	Shrub	Open tussock- and shrubland
C. curta	Nationally Endangered	Shrub	Rock outcrops, alluvium
C. hollowayi	Nationally Critical	Dwarf shrub	Rock outcrops
C. juncea	Nationally Endangered	Dwarf Shrub	Alluvium, rock outcrops
C. kirkii	Nationally Endangered	Climber	Divaricating shrubland
C. muritai	Nationally Critical	Tree	Coastal forest
C. stevensonii	Gradual Decline	Tree	Rock outcrops, alluvium
C. vexillata	Serious Decline	Dwarf shrub	Alluvium, moraines

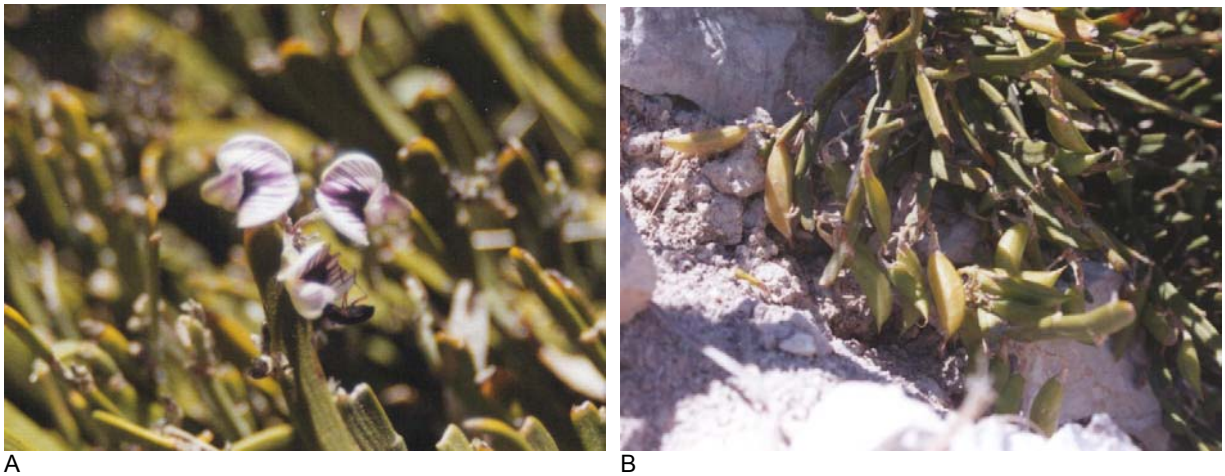
In the following, brief descriptions of the ten study species are provided to introduce their main characteristics. The morphological and phenological information is based on Purdie (1985) and Heenan (1995, 1996b), who give more detailed descriptions of each species, as well as on my own observations. Descriptions of juveniles are based on Heenan (1997) and personal observations. Distribution data were made available by the herbaria at Landcare Research, Lincoln (Allan Herbarium), the War Memorial Museum, Auckland, and Te Papa, Wellington, as well as by Department of Conservation staff. Conservation status follows de Lange et al. (1999). Additional sources are indicated in the text.

The distribution maps included in the descriptions are based on the NZ Topographical Map Series 260 (1 : 50 000), with each sheet being further subdivided into 10 x 10 km grid cells. If a species has been recorded at least once within the area of a grid cell, this is illustrated using the appropriate symbol. The maps do not reflect the total number of populations known for each species, as one grid cell can contain several populations. Lists of the individual locations known for each species are provided in Appendix 1, together with a transparency that can be used to identify the relevant mapsheets in the distribution maps.

3.3.1 *Carmichaelia astonii* (Fig. 3.3, Fig. 3.4, Fig. 3.5)

Growth form:	dwarf shrub, up to 20 cm tall and 50 cm wide
Growth habit:	relatively open, spreading, non-rhizomatous
Cladodes:	strongly compressed, 4-8 mm wide, up to 9.5 cm long, green to green-bronze
Flowers:	Dec – Jan, c. 10 mm long, white with purple marks
Pods:	Dec – April, 14-21 x 4-6 mm, light grey or brown, laterally compressed, valves inflated, indehiscent or slightly dehiscent at base, beak 1-2 mm long, pungent, some pods remain intact besides adult plant for at least one year
Seeds:	c. 3 mm, (4-)6-8 per pod, olive-green, green-yellow or dull yellow, occasionally mottled black
Juveniles:	no distinct juvenile form, first shoots erect, compressed, sometimes with simple leaves
Current range:	restricted to areas in Marlborough where Amuri limestone emerges as base rock
Historic range:	as current range
Population size:	unknown, several ‘moderate’ sized populations (Heenan 1995)
Conservation status:	Range Restricted

Fig. 3.3: *C. astonii*, Ward, southern Marlborough.



A B

Fig. 3.4: A - Flowers of *C. astonii*, Ward, with foraging beetle (*Parisopalpis* sp.); B - Immature pods of *C. astonii*, Ward.

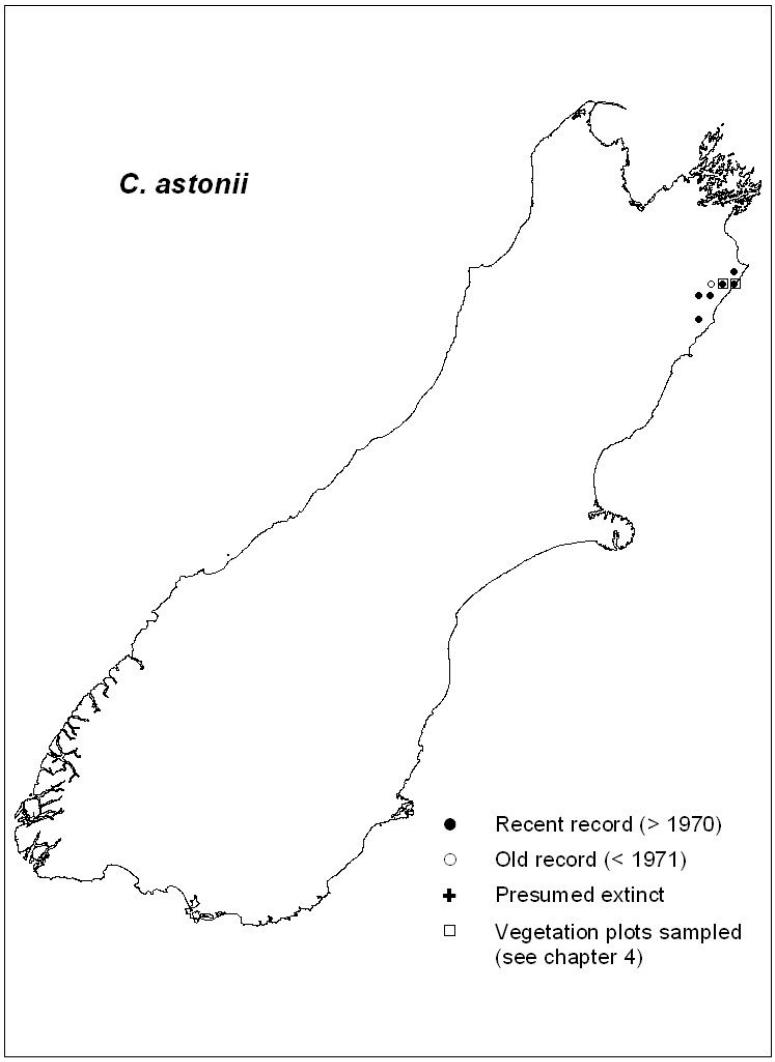


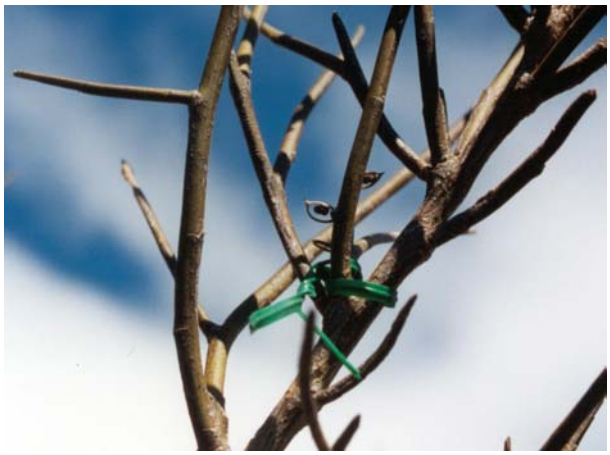
Fig. 3.5: Historical and current distribution of *C. astonii*. The species is restricted to areas in Marlborough, where Amuri limestone emerges as base rock.

3.3.2 *Carmichaelia australis* (Fig. 3.6, Fig. 3.7, Fig. 3.8)

Growth form:	shrub, 2-3(-8) m tall
Growth habit:	upright or spreading, sometimes rhizomatous
Cladodes:	very variable, 1.5-4 mm wide, 3-20 cm long, rounded or compressed, obtuse-tipped or pungent, yellow-green, brown-green, or bright green
Flowers:	Oct-Feb, c. 5 mm long, white with purple marks
Pods:	Nov-May, 6.5-15 x 2-5.5 mm, laterally compressed, brown, grey, or black, small apical beak, valves dehiscent
Seeds:	2-4 mm, 1-5 per pod, black, green, yellow-green, or orange, often mottled with black, some seeds remain on the plants, attached to replum, for at least one year
Juveniles:	several prostrate to decumbent shoots with simple, heart-shaped leaves, plants brown-green, sometimes with white mottling
Current range:	widespread throughout the North and South Island of New Zealand, in the east south to a latitude of c. 45°
Historic range:	as current range
Population size:	unknown
Conservation status:	not listed, common

Fig. 3.6: *C. australis*, Tone Valley, southern Marlborough.

A



B

C

Fig. 3.7: A - Flowers of *C. australis* pollinated by a butterfly, Godley Head, Canterbury; B - Pods of *C. australis*, Mackenzie Pass, Canterbury, seeds stay attached to the replum after valves have been detached; C - Juveniles growing in the shelter of a rock, Godley Head, Canterbury.

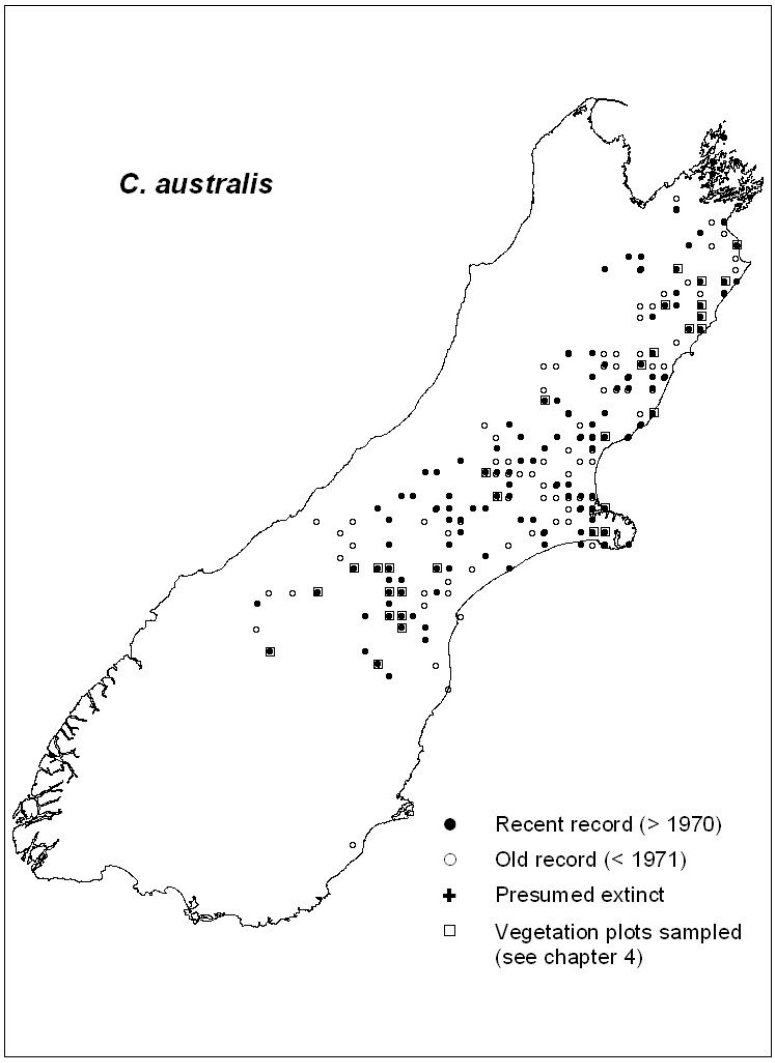


Fig. 3.8: Historical and current distribution of *C. australis* in the South Island of New Zealand. Only records in the east of the island are shown. The species also occurs in in the west from northwest Nelson to Fiordland (see Heenan 1996b).

3.3.3 *Carmichaelia crassicaule* (Fig. 3.9, Fig. 3.10, Fig. 3.11)

Growth form:	shrub, up to 2 m tall
Growth habit:	upright, sparsely branched, sometimes rhizomatous
Cladodes:	stout, mostly rounded, up to 10 mm wide, deep longitudinal grooves
Flowers:	Dec-Jan, c. 6 mm long, lavender
Pods:	Jan-April, c. 6 x 3-4 mm, densely hairy, indehiscent, shed quickly at maturity
Seeds:	c. 2 mm, 1-2 per pod, green
Juveniles:	erect to drooping, strongly compressed, dark brown, hairy, with simple green leaves
Current range:	eastern South Island from southern Marlborough to Central Otago
Historic range:	same as current range
Population size:	unknown, many scattered, small populations
Conservation status:	Gradual Decline

A

B

Fig. 3.9: A - *C. crassicaule*, Poolburn, Central Otago; B - Detail of shoot. Cladodes show deep longitudinal grooves with distinct white hairs.

A B

Fig. 3.10: A - Flower buds on *C. crassicaule*, Porters Pass; B - Juvenile plant of *C. crassicaule* growing in shelter of a rock, Remarkables, Central Otago.

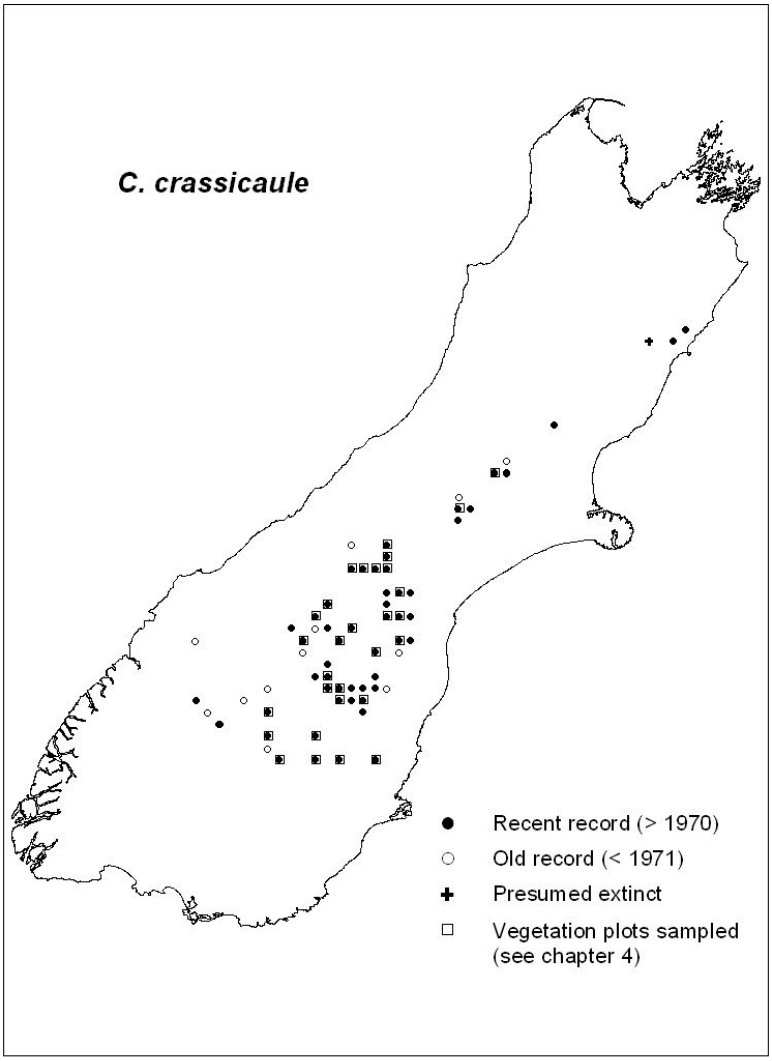


Fig. 3.11: Historical and current distribution of *C. crassicaule.* The range of this species extends with scattered populations from southern Marlborough to Central Otago.

3.3.4 *Carmichaelia curta* (Fig. 3.12, Fig. 3.13, Fig. 3.14)

Growth form:	shrub, up to 1 m tall
Growth habit:	sparsely branched, upright to spreading, rhizomatous
Cladodes:	rounded, 2.5 mm wide, up to 45 cm long, olive green to brown-green, with purplish bloom when young
Flowers:	Oct-July, c. 4 mm long, white with purple marks
Pods:	Jan-Aug, 4-5.5 x 2-2.5 mm, dorsiventrally compressed, obovate in top view, brown or straw-coloured, indehiscent, beak 1-2 mm long, pungent, pods shed quickly at maturity
Seeds:	1.5-2 mm, 1-2 per pod, olive-green or light brown with black mottling
Juveniles:	several erect to decumbent, very leafy shoots, leaves with several pairs of leaflets, mottled grey-green to bronze
Current range:	Mackenzie Basin, upper Waitaki Valley, and North Otago
Historic range:	wider than current range with populations in coastal areas near Oamaru and inland areas of Central Otago
Population size:	at least 1649 individuals in Mackenzie Basin and upper Waitaki Valley area (Grove 2001)
Conservation status:	Nationally Endangered

Fig. 3.12: *C. curta*, Black Jack's Island, Lake Benmore, southern Canterbury.

A B

Fig. 3.13: A - Juvenile of *C. curta*, Waitaki Valley, roadside; B - Flowers of *C. curta* pollinated by native bee, Waitaki Valley, roadside.

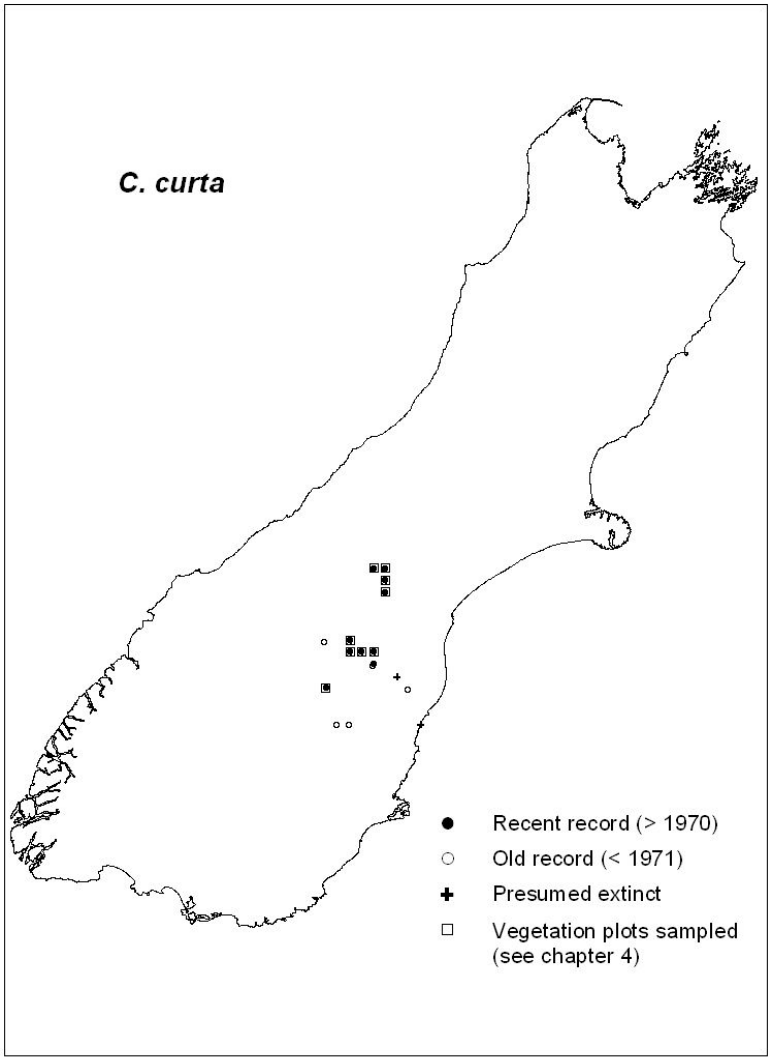


Fig. 3.14: Historical and current distribution of *C. curta*. The historic range of *C. curta* extended to coastal areas in Canterbury and inland Central Otago.

3.3.5 *Carmichaelia hollowayi* (Fig. 15, Fig. 3.16, Fig. 3.17)

Growth form:	dwarf shrub, up to 50 cm tall and 2 m wide
Growth habit:	relatively open, sprawling, rhizomatous
Cladodes:	3-7 mm wide, 5-10 cm long, erect to spreading, plano-convex in cross-section, rarely rounded, apex obtuse and rounded, yellow-green to green
Flowers:	Nov-Dec, c. 7 mm long, white with purple marks
Pods:	Jan-May, 8-11 x 4.8-6 mm, laterally compressed, drooping, light grey to yellow brown, valves flat, both valves dehiscent at base, small apical beak
Seeds:	c. 2.5 mm, 1(-2) per pod, yellow-green or green with black mottling, detaching
Juveniles:	erect to decumbent, leafy shoots, brown to green in colouring often with white or bronze mottling
Current range:	restricted to outcrops of Otekaieke limestone on the southern side of the Waitaki Valley, South Canterbury
Historic range:	same as current range
Population size:	currently four populations known with a total of around 250 plants
Conservation status:	Nationally Critical

A

B

Fig. 3.15: *C. hollowayi*, Awahokomo, southern Canterbury. A - Cladodes are 3-7 mm wide and erect; B - Plants form mats of suckering shoots.

A

B

Fig. 3.16: A - Flowers of *C. hollowayi*; B - Juvenile shoot of *C. hollowayi*, both photos: Awahokomo, southern Canterbury.

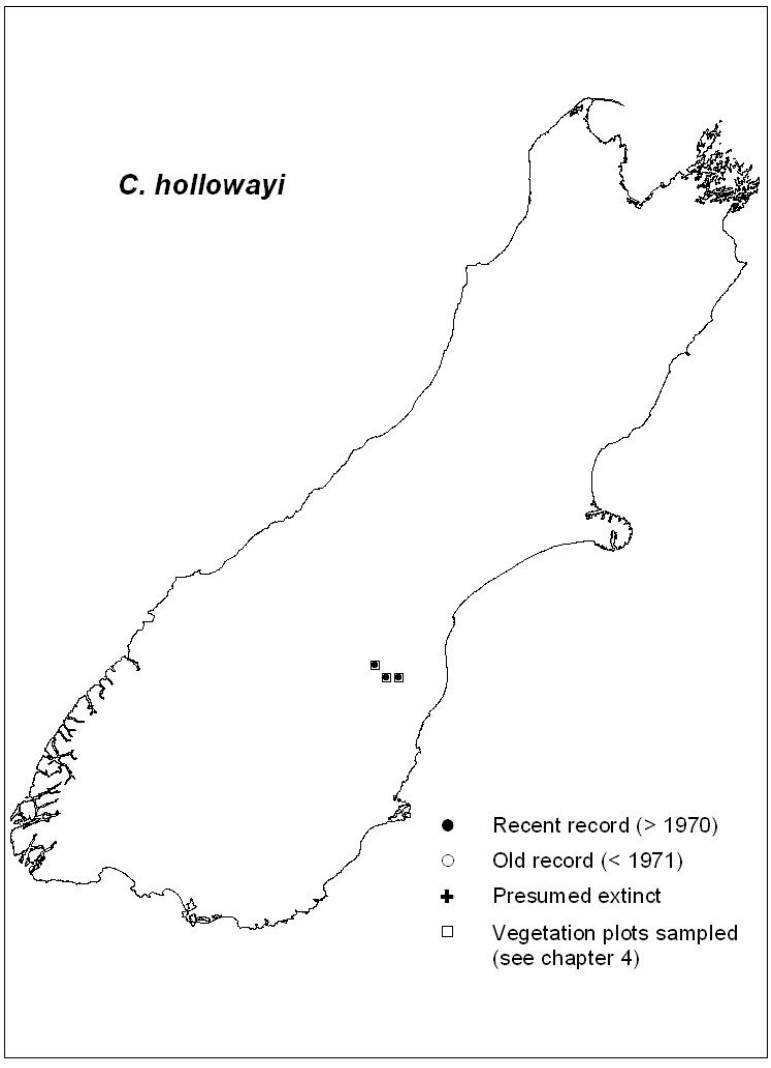


Fig. 3.17: Historical and current distribution of *C. hollowayi.* The species is restricted to outcrops of Otekaieke limestone on the southern side of the Waitaki Valley.

3.3.6 *Carmichaelia juncea* (Fig. 3.18, Fig. 3.19, Fig. 3.20)

Growth form:	dwarf shrub, up to 20 cm tall and 1.5 m wide
Growth habit:	prostrate with branches spreading on the ground, not rhizomatous
Cladodes:	linear, 2 mm wide, up to 16 cm long, compressed, often dark on the upwards facing side and green towards the ground
Flowers:	Oct-Jan, 4-5 mm long, white with purple marks
Pods:	Nov-March, 3.6-6 x 2 mm, weakly dorsally compressed, valves inflated, dark grey to black, indehiscent to weekly dehiscent at base, beak 0.5 mm long, pungent,
Seeds:	1-1.5 mm, 2-4(-6) per pod, brick red, orange, olive green, or green-yellow, often with black mottling
Juveniles:	prostrate to decumbent with brown-green to whitish leaves, often with freckled appearance
Current range:	localised in South Westland and Northwest Nelson
Historic range:	much wider than current range with populations in Marlborough, Canterbury, Otago, Fiordland, and one record from Hawkes Bay
Population size:	several hundred individuals in three populations in South Westland, and seven individuals in NW Nelson
Conservation status:	Nationally Endangered

A B

Fig. 3.18: *C. juncea*, Waiho River, South Westland. A - Large adult plant; B - Flowers.

A B

Fig. 3.19: A - Seedlings of *C. juncea*, Waiho River, South Westland; B - Juvenile plant, Welcome Flat, South Westland.

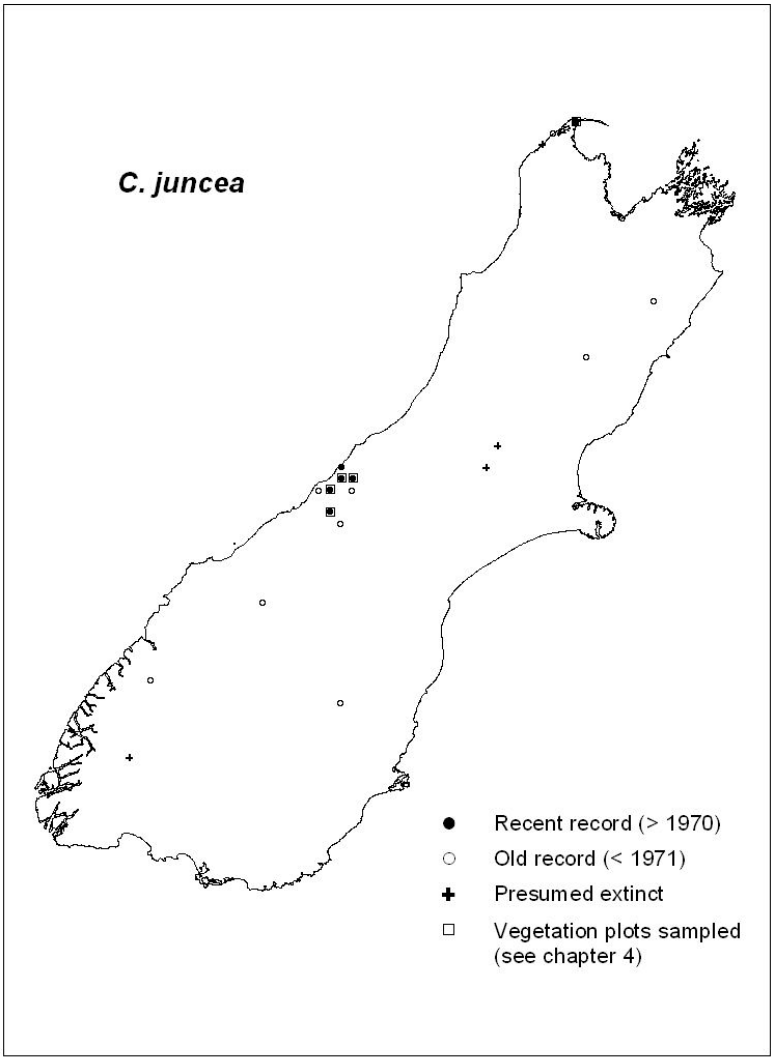


Fig. 3.20: Historical and current distribution of *C. juncea* in the South Island of New Zealand. The species is presently restricted to four populations in western areas, but used to be more widespread in the past.

3.3.7 *Carmichaelia kirkii* (Fig. 3.2, Fig. 3.21, Fig. 3.22, Fig. 3.23)

Growth form:	climber, up to 3 m tall
Growth habit:	usually entangled in associated small leaved shrubs, occasionally self-supporting, leafy in high humidity
Cladodes:	1.7-3 mm wide, up to 40 cm long, rounded, spreading, branching at right angles, green to bronze, sometimes hairy,
Flowers:	Nov-Jan, c. 9 mm long, white to off-white with purple marks
Pods:	Jan-June, 12-18 x 4-5.8 mm, laterally compressed, dark brown or grey-brown, both valves partially dehiscent and remaining attached, large, prominent apical beak, 3-6 mm long, pungent
Seeds:	2-3.5 mm, 2-5 per pod, white, off-white, or sometimes light pink, with black or dark purple mottling, some seeds remain on the plants inside half open pods for at least one year
Juveniles:	erect to decumbent, leafy, stems stout, usually terete, brown to grey, trifoliate leaves with obcordate leaflets, green, often with red margins
Current range:	eastern parts of the South Island from Marlborough to Central Otago
Historic range:	same as current range, but several populations are known to be extinct
Population size:	several large populations (> 300 individuals) in the Benmore Range, Mackenzie Basin (Wardle 2000a), smaller populations in other areas
Conservation status:	Nationally Endangered

A B

Fig. 3.21: A - *C. kirkii*, Scrubby Creek, Benmore Range, southern Canterbury; B - Juveniles, Blackstone Gully, Central Otago.

A B

Fig. 3.22: A - Mature pod of *C. kirkii.* Seeds remain inside the pods after opening of the valves; B - Stem base; both photos: Scrubby Creek, Benmore Range, southern Canterbury.

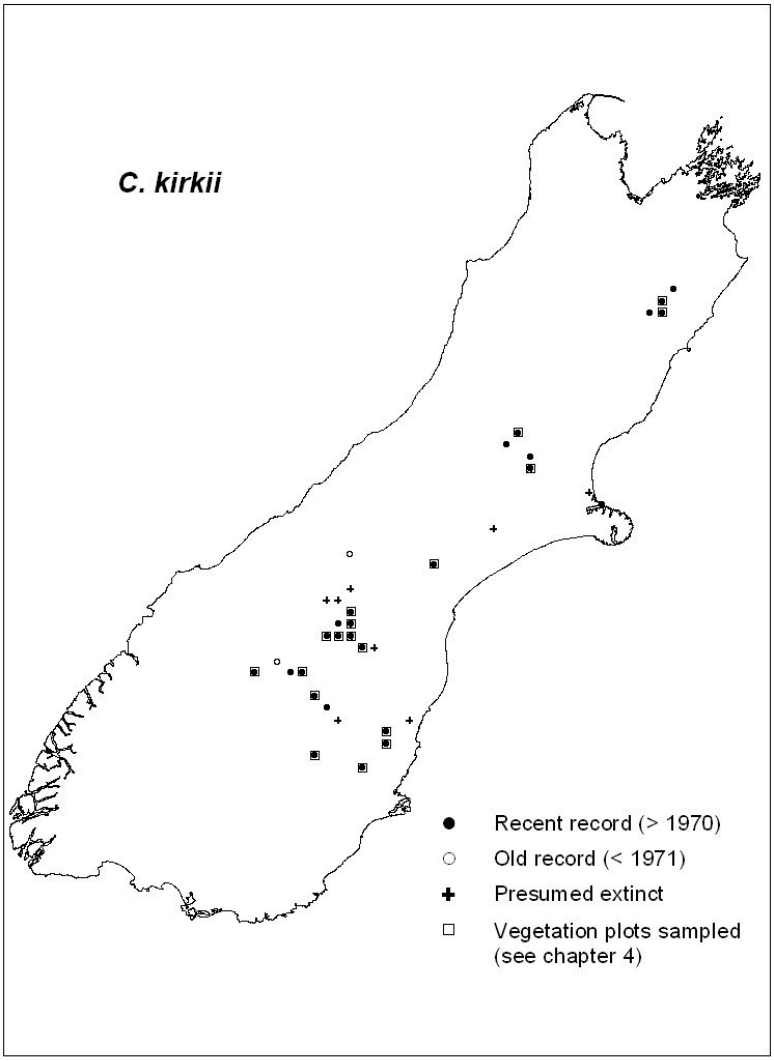


Fig. 3.23: Historical and current distribution of *C. kirkii*. While the species occurs still widespread along the east of the South Island, a number of populations recorded in the past have become extinct.

3.3.8 *Carmichaelia muritai* (Fig. 3.24, Fig. 3.25)

Growth form:	tree, up to 6 m tall
Growth habit:	single or multiple stem tree, branches in crown erect to drooping
Cladodes:	2.5-3.5 mm wide, rounded, distinctly grooved, upper erect, lower drooping
Flowers:	Dec-Jan, every second year, c. 5 mm long, white with purple marks, in erect racemes
Pods:	Jan-Feb, 3.5 x 1.8 mm, hairy, indehiscent, apical beak 1 mm, pungent, pods shed quickly at maturity
Seeds:	1 mm, 1 per pod, yellow-green
Juveniles:	erect, white to brown, hairy, leafless
Current range:	two populations in Clifford Bay, Marlborough
Historic range:	unknown, species was only described in 1985 (Purdie 1985)
Population Size:	42 adults and 22 immature plants at Seaview (excl. planted), at least 20 adults and immature plants at White Cliffs
Conservation Status:	Nationally Critical

A

B

Fig. 3.24: A - *C. muritai*, White Bluffs, southern Marlborough; B - Flowers of *C. muritai*, Seaview, southern Marlborough.

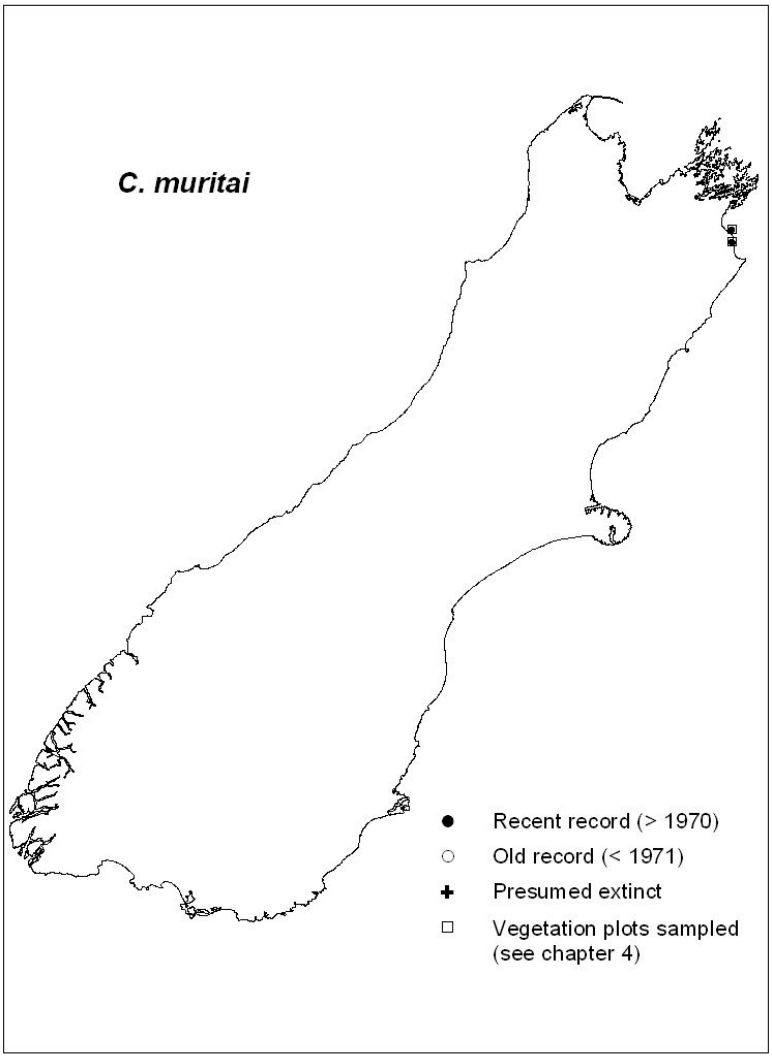


Fig. 3.25: Current distribution of *C. muritai*. The species was only described in 1985, and historical records do not exist.

3.3.9 *Carmichaelia stevensonii* (Fig. 3.1, Fig. 3.26, Fig. 3.27, Fig. 3.28)

Growth form:	tree, up to 7 m tall
Growth habit:	single or multiple stem tree, branches in crown drooping
Cladodes:	2.5-3.5 mm wide, rounded, shallowly grooved, drooping
Flowers:	Dec-Jan, possibly not every year, pale lavender with darker veins, c. 5 mm long, in drooping racemes
Pods:	Jan-April, 6 x 3-4 mm, hairy, indehiscent, short apical beak, some pods can remain on the plant for at least one year
Seeds:	c. 2 mm, 1-3 per pod, green
Juveniles:	erect, shoots compressed, up to 2 mm wide, light brown, with few dark green, simple leaves
Current range:	Inland and Seaward Kaikoura Ranges, Marlborough
Historic range:	slightly wider than current range, extending to lower altitudes
Population size:	unknown
Conservation status:	Gradual Decline

Fig. 3.26: *C. stevensonii* in cultivation, B. & N. Ledgard, Loburn, South Island, New Zealand.

A B

Fig. 3.27: A - Flowers of *C. stevensonii*, garden of B. & N. Ledgard, Loburn; B - Juvenile plant growing in creek bed gravel, George Stream, southern Marlborough.

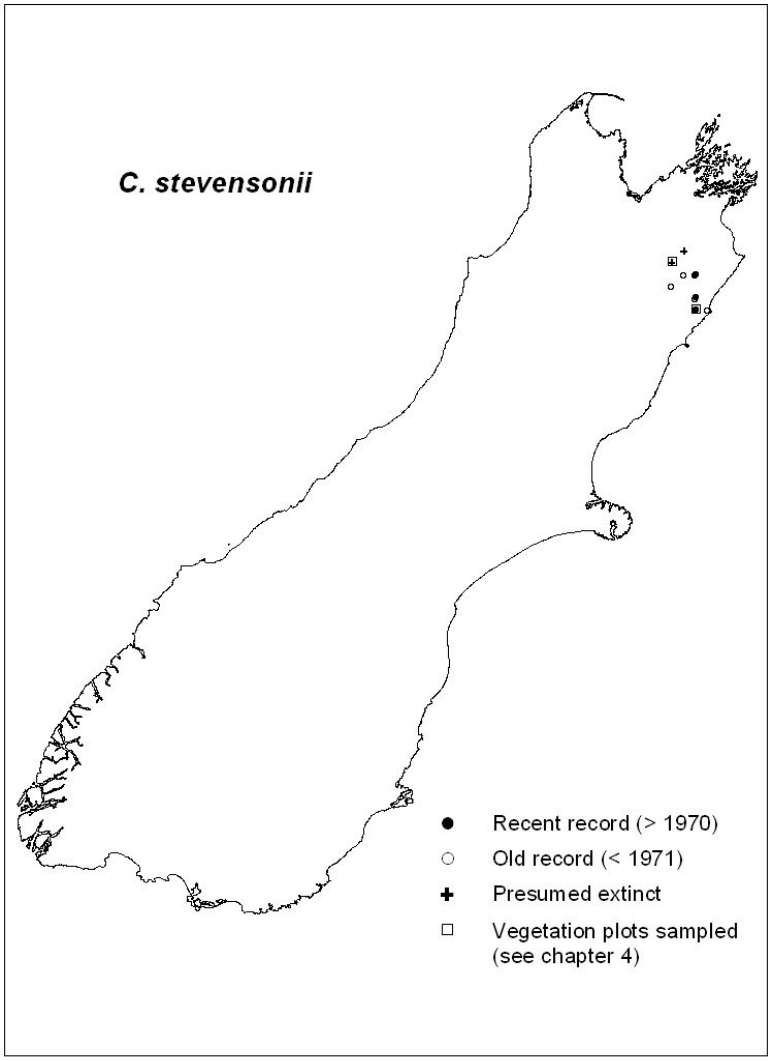


Fig. 3.28: Historical and current distribution of *C. stevensonii*. The species is restricted to southern Marlborough.

3.3.10 *Carmichaelia vexillata* (Fig. 3.1, Fig. 3.29, Fig. 3.30, Fig. 3.31)

Growth form:	dwarf shrub, up to 15 cm tall and 60 cm wide
Growth habit:	dense mats, not rhizomatous
Cladodes:	subterete to compressed, erect to spreading, 2-4 mm wide, up to 9.5 cm long, green and green-yellow, often with orange tips, apex obtuse
Flowers:	Nov-Jan, 8-10 mm long, white with purple marks
Pods:	Dec-March, 12-17 x 3-4 mm, dark brown or light grey, indehiscent or one valve slightly dehiscent at base, laterally compressed, valves inflated, small apical beak, pods remain intact besides adult plant for at least one year
Seeds:	2-2.5 mm, (4-)9-11(-13) per pod, yellow, yellow-green, or olive-green with black mottling
Juveniles:	no distinct juvenile form, first shoots green, strongly compressed, zigzagging
Current range:	eastern South Island with stronghold in South Canterbury and scattered populations in Marlborough and northern Otago
Historic range:	same as current range
Population size:	unknown, but likely to total several thousand
Conservation status:	Serious Decline

Fig. 3.29: *C. vexillata*, Pukaki-Ohau Canal, Mackenzie Basin.

A

B

Fig. 3.30: A - Cladodes of *C. vexillata*, Balmoral Station, Mackenzie Basin; B - Pods, Pukaki-Ohau Canal, Mackenzie Basin.

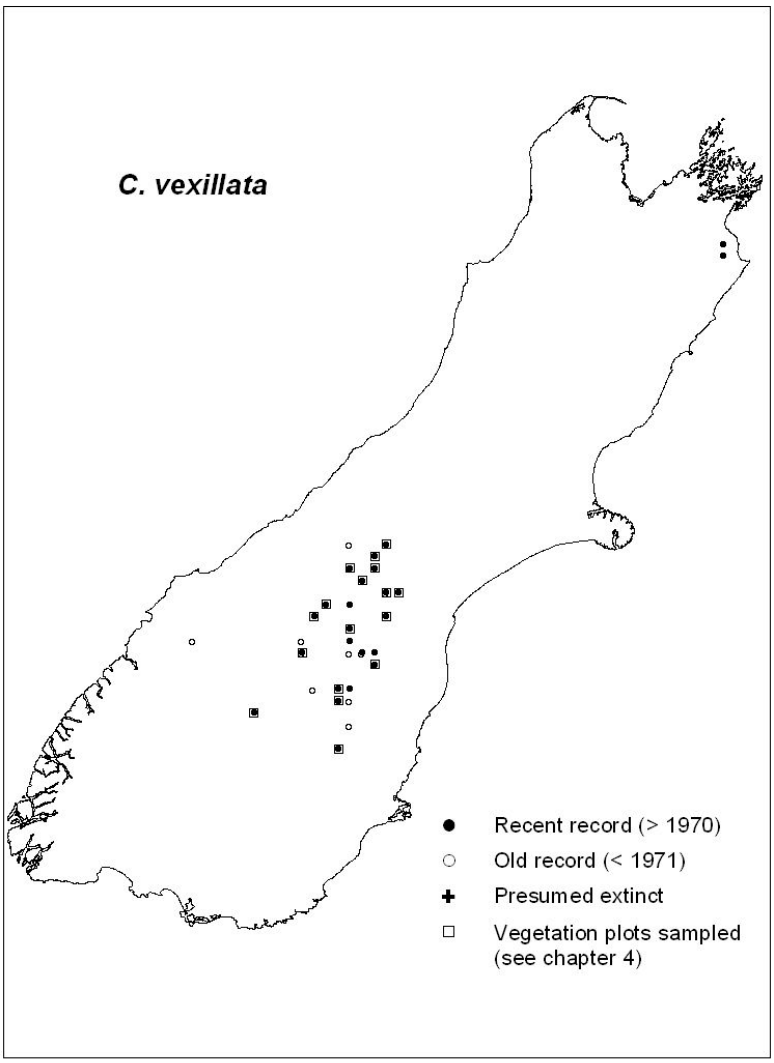


Fig. 3.31: Historical and current distribution of *C. vexillata*. The species shows disjunct distribution with most of its populations in southern Canterbury and Otago, and two sites in Marlborough.

4 Habitat and Community Ecology of *Carmichaelia*

4.1 Introduction

This chapter explores the habitats and plant communities the ten *Carmichaelia* species currently occur in, with the aim of gaining a deeper understanding of their ecology, in particular, regarding similarities and differences between the various species.

Knowledge of the ecology of threatened species is essential, if their conservation management is to be successful. The long-term recovery of threatened species, i.e. the establishment of self-sustaining populations, is only achievable when populations exist within appropriate habitats (de Mauro 1994; Pavlik 1994). While management focusing on threatened species independent from their habitats can ensure the immediate survival of plants, e.g. through fencing of individuals to protect them from herbivore damage, such measures will only deliver short-term solutions, leaving the need for ongoing management. Norton and Reid (1997) demonstrate this limitation of strictly species-oriented management on the example of New Zealand and Australian mistletoes. Here, the consideration of mistletoe ecology with respect to habitat requirements and the dynamics of predation and disturbance could provide long-term solutions for the conservation of rare mistletoes in New Zealand, as well as for the control of pest mistletoes in Australia. The need for an understanding of species' ecology has, furthermore, become apparent in the conservation of a number of threatened plant species (e.g., Frost 1981; Morgan and Norton 1992; Naito and Nakagoshi 1995).

The ecology of *Carmichaelia* species is not very well understood. While their phylogeny, taxonomy, morphology and anatomy have been extensively studied (e.g., Heenan 1995, 1996a, b, 1997a, b, 1998a, b; Wagstaff et al. 1999), knowledge of habitats and plant communities is limited. Descriptions of habitats are restricted to relatively broad statements, such as 'rock outcrops', 'river terraces' or 'disturbed sites' (Heenan 1995, 1996b; Dopson et al. 1999). Similarly, plant communities *Carmichaelia* species occur in have mainly been defined in very general terms. For example, *C. stevensonii* has been described as typical for 'heath' (Wardle 1991), and *C. crassicaule* as species of 'tussock grassland' and 'montane scrub' (Heenan 1997b). The habitat of *C. kirkii* seems clearer, as it is known to be associated with divaricating shrubs forming mature shrubland communities commonly known as 'grey scrub' (Wardle 1991; Heenan 1996b). Probably best understood are *C. astonii* and *C. hollowayi*, as these two species are part of the basicole element within the New Zealand flora (*sensu* Molloy 1994; Druce and Williams 1989, Wardle 1991). Their specialisation to

limestone substrate appears as their main ecological characteristic and, furthermore, explains the limited geographical distribution of these two species.

Some inferences on the conditions in *Carmichaelia* habitats can be drawn from their physiology and anatomy. As nitrogen-fixing plants they are likely to grow under relatively infertile conditions (Heenan 1997a), and the strongly xeromorphic wood anatomy suggests adaptation to drought (Heenan 1997b). Heenan (1997a) relates juvenile morphology to preferred habitat conditions, and suggests shaded forest margins and tall scrub habitats as typical for species with erect juveniles (*C. muritai*, *C. stevensonii*, *C. crassicaule*), while the decumbent juveniles characteristic of most other species of *Carmichaelia* indicate adaptation to open vegetation.

One difficulty in the attempt to understand the ecology of *Carmichaelia* species arises from the fact that the current habitats might not be in equilibrium with the actual requirements of the species, as the present habitats are not the ones in which the species evolved (Heenan 1997b). Since the beginning of human settlement, New Zealand ecosystems have undergone drastic changes, altering the distribution, structure and composition of indigenous plant communities. Most *Carmichaelia* presently occur in highly modified areas, such as agricultural landscapes, and the persistence of their populations is doubtful, as regeneration has often not been observed (Dopson et al. 1999; but see Williams et al. 1996). However, the conservation management of *Carmichaelia* species needs to focus on the present habitats of the species, as the extent and characteristics of the original habitats are unknown. This highlights further the need for a better understanding of the ecology of the *Carmichaelia* species, and of their interaction with today's habitats and environment.

4.2 Objective and Research Approach

The objective of this part of the study was to provide detailed descriptions of the habitats and plant communities in which *Carmichaelia* species currently occur, with the aim of gaining a better understanding of the ecology of the various species. Using a quantitative-descriptive approach, habitat characteristics and the composition of associated plant communities were assessed. Emphasis was further laid on the detection of regeneration, as indicator for the viability of populations. The analysis of the current habitats and plant communities allowed insight into the habitat requirements of the *Carmichaelia* species, providing guidelines for their successful conservation management. Furthermore, the results of the study allowed drawing inferences on potential threats to the *Carmichaelia* species in their present habitats.

4.3 Methods

4.3.1 Data Collection

To characterise the present habitats of the ten *Carmichaelia* species data from 255 vegetation plots were collected during a period of three years, from April 1999 to March 2002. The methodology was based on that described by Braun-Blanquet (1964), with modifications as suggested by Allen and McLennan (1983), and Allen (1992) to comply with the required format for analysis using the PC RECCE software package (Hall 1992).

Selection and Size of Vegetation Plots

The vegetation data were recorded in habitats of the ten *Carmichaelia* species with the attempt to visit all presently known populations of the species. Where this was not possible, the locations were spread over the geographical as well as altitudinal range of the species and, as far as known, over different habitat types, to attain a representative sample of the ecological ranges of each species. The distribution maps presented in section 3.3 provide an overview over the distribution of the various species and the locations visited during this study. Grid references for the individual plots are provided in the locations lists in Appendix 1.

In each population, the habitat of the *Carmichaelia* species was first thoroughly examined by walking through the area and identifying characteristics of the site and the vegetation. Then plot locations were chosen in a way that they included *Carmichaelia* plants and at the same time were representative of the respective vegetation type. Plots were homogeneous with respect to both, vegetation structure and abiotic conditions as far as observable. Obvious disturbances, such as animal tracks, and other habitat discontinuities were avoided.

Plots sizes were selected according to the following guidelines:

Pioneer vegetation and grassland of riverflats:	6-12 m^2,
Short tussock grassland:	16-25 m^2,
Tall tussock grassland:	25-30 m^2,
Low scrub (-3 m):	35-50 m^2,
Tall scrub:	100 m^2.

These sizes were assumed to be sufficient to attain representative samples of the respective vegetation types. Plot sizes varied with local conditions. Where *Carmichaelia* occurred in

small remnants of vegetation, smaller plots had to be used, often comprising the whole stand. If this was the case, where possible, data from several smaller plots were combined to form one sample, their areas adding up to the required plot size. In scrub vegetation the plot boundaries were located at least 0.5 m from the edge to avoid the immediate transition zone with the adjacent vegetation type. A wider distance to the edge was usually not possible, as stands were very small.

Recorded Data

The following data were recorded for each vegetation plot:

Header record:
The header record included *Carmichaelia* species, date, location, grid reference (using New Zealand Topographical Map Series 260 (1:50 000)), altitude, slope, aspect, physiography (distinguished as ridge, face, gully, terrace), habitat type, herbivore damage and likely herbivores present.

Cover:
% cover was estimated for vascular plants, separating an upper and lower shrub tier from the ground tier, and for moss and lichen, litter, bare ground, and rocks > 10 cm. An upper or lower shrub tier were only distinguished, if their cover was ≥ 20%. Moss and lichen cover only included those plants growing on soil.

Height:
Vegetation height was only assessed, when a shrub tier was present. The lower height limit for the shrub tier was set at 0.80 m. The limit between upper and lower shrub tier varied with the structure of the vegetation type. The mean top height of the stands was also recorded.

Vascular plant species and cover:
All vascular plant species present in the plot were recorded with cover estimates, separated by tiers. The following cover classes were used:

1 : 1 - 5 plants, < 6% cover
2 : > 6 plants, < 6% cover
3 : 6 - 25% cover
4 : 26 - 50% cover
5 : 51 - 75% cover
6 : 76 - 100% cover.

Juveniles of the *Carmichaelia* species were recorded separately to assess active regeneration. For the rhizomatously growing species, observation of juveniles did not necessarily imply sexual regeneration, as young rhizomatous shoots were observed to possess juvenile morphology. For the two dwarf shrub species without a distinct juvenile stage, *C. astonii* and *C. vexillata*, active regeneration was assumed when very small plants with a plant diameter of less than 2 cm, or with less than five cladodes were found in the plots.

4.3.2 Plant Identification, Nomenclature and Syntaxonomie

Plants were identified using the following books and articles:

Allan (1982), Bishop (1990), Brownsey and Smith-Dodsworth (1989), Edgar and Connor (2000), Healy and Edgar (1980), Lloyd (1972), Mark and Adams (1979), Molloy et al. (1999a, b), Moore (1976), Poole et al. (1994), Rothmaler (1994a, b), Webb et al. (1988), Wilson (1994, 1996), and Wilson and Galloway (1993).

Identifications were also undertaken with the help of the Allan Herbarium at Landcare Research, Lincoln (CHR), and its staff, in particular Peter Heenan. Jo Ward (University of Canterbury, Christchurch), Nick Head, Shannel Courtney, and Phil Knightbridge (all Department of Conservation) helped with further plant identification.

Species names followed the listing in Parsons et al. (1998) for all vascular plants except the *Carmichaelia* species (Heenan 1995, 1996b, 1998a), grasses (Edgar and Connor 2000), and Cyperaceae and Juncaceae (Healy and Edgar 1980). Ferns and lycopods were named as in Brownsey and Smith-Dodsworth (1989).

Plant communities were named following the principles suggested by Atkinson (1985), using the names of the one or two most dominant species together with a structural term (e.g., grassland) defined by the dominant growth form. The following bracket code was combined with the species names to indicate their average cover in the community:

species name without brackets	cover ≥ 20%,
(species name)	cover 10 - 19%
[species name]	cover 1 – 9%.

Different types within a plant community were distinguished by the dominant indicator species. In contrast to Atkinson's naming system, preference was given to botanical species names rather than common names.

As the sampling plots were subjectively selected in habitats of *Carmichaelia* species, the units described as communities in this study might not be representative of communities in a more general, vegetation oriented context. In particular, abundance and dominance relationships are likely to vary considerably depending on local site conditions. To establish a connection with the broader pattern of plant communities in the South Island of New Zealand, the distinguished units, therefore, were described in the context of other vegetation studies, where related references could be found.

4.3.3 Analysis

The plot data were analysed using the software package PC - RECCE (Hall 1992), which includes the two-way indicator species analysis programme TWINSPAN (Hill 1979). This is a multivariate analysis programme providing a two-way classification of plot and species data by performing repeated ordination and division of the data. Each level of division includes an indicator species analysis to characterise the resulting classification. The ten *Carmichaelia* species were excluded from this analysis, as the sample plots had been subjectively chosen to include these species.

For the construction of individual importance values for each species in each plot, the cover classes were converted to cover weights chosen as the percentage midpoint of each class, except for class 1 which received a cover weight of 1.0. As the tier weights were set at 1 for all tiers, the importance value of a species was calculated as the sum of its cover weights over all tiers in a plot. In the TWINSPAN analysis the pseudo-species cut levels were chosen at 0.0, 3.0, 15.0, 37.5, and 62.5, aiming at a relatively even spread of the species over the different cut levels. For all other settings, the defaults included in the PC RECCE/TWINSPAN software were used.

The classifications suggested by TWINSPAN were examined in view of the ecological context of the indicator species and patterns observed in the field, to ensure results were ecologically meaningful. Based on these considerations, the final levels of division and allocation of plots were decided. Alterations were carried out following the methodology for phyto-sociological tablework as described by Braun-Blanquet (1964; see also Dierssen 1990; Dierschke 1994). Further indicator species were selected for each plant community, the main

criterion being the frequency of the species in the community. Frequency was divided into five categories (based on Braun-Blanquet 1964):

I	-20%
II	> 20-40%
III	> 40-60%
IV	> 60-80%
V	> 80%.

Generally, a species sufficiently differentiated one plant community from another if the frequency in the considered community was above 40% (i.e., class III or higher), while its frequency in the other community was at least two categories lower (e.g., frequency III differentiated against I, IV against II and I). In communities represented by fewer than five plots the criteria were chosen to be more restrictive, with the indicator species reaching at least frequency class IV with a margin of three classes against the contrasted community.

The initial analysis using all 255 sample plots resulted in the distinction of seven main groups of plots. A second step of the analysis divided these groups into finer units. This second step was performed separately for each of the main groups, to reduce the noise within the data at this level of analysis. Summary tables including habitat characteristics, mean number of species per plot and mean cover values were calculated for the resulting classification of plant communities. The cover values in these tables represent the mean cover over all plots in the respective community, based on the midpoints of the initially assigned cover classes. This leads to an underestimation for species and tiers with very high cover values (> 87.5%), as the maximum mean is 87.5% (cover class 6). For tiered vegetation types, mean top height was calculated for the upper most stratum present in the majority of plots.

The derived plant communities were analysed by setting their floristic and structural characteristics in relation to the plant and vegetation ecology of New Zealand, with the aim to gain insight into the dynamics of the communities and their role as habitats for the *Carmichaelia* species.

4.4 Results

In the first step of the analysis, the data collected for the ten *Carmichaelia* species in a total of 255 vegetation plots were divided into seven main, floristically and structurally distinct, vegetation types (Fig. 4.1). The names chosen for these types reflect their main characteristics with respect to habitat or physiognomy.

Pioneer vegetation on alluvial flats of South Westland (19 plots) was separated from the other vegetation types by the presence of the pioneering herbs *Raoulia hookeri, Epilobium brunnescens*, and *E. microphyllum.* A single plot, sampled in the only known population of *C. juncea* in Northwest Nelson, was separated as cliff face vegetation by the presence of *Coprosma acerosa*. The 102 plots characterised as grassland vegetation were connected by the presence of *Hieracium pilosella, Festuca novae-zelandiae* and *Poa colensoi*.

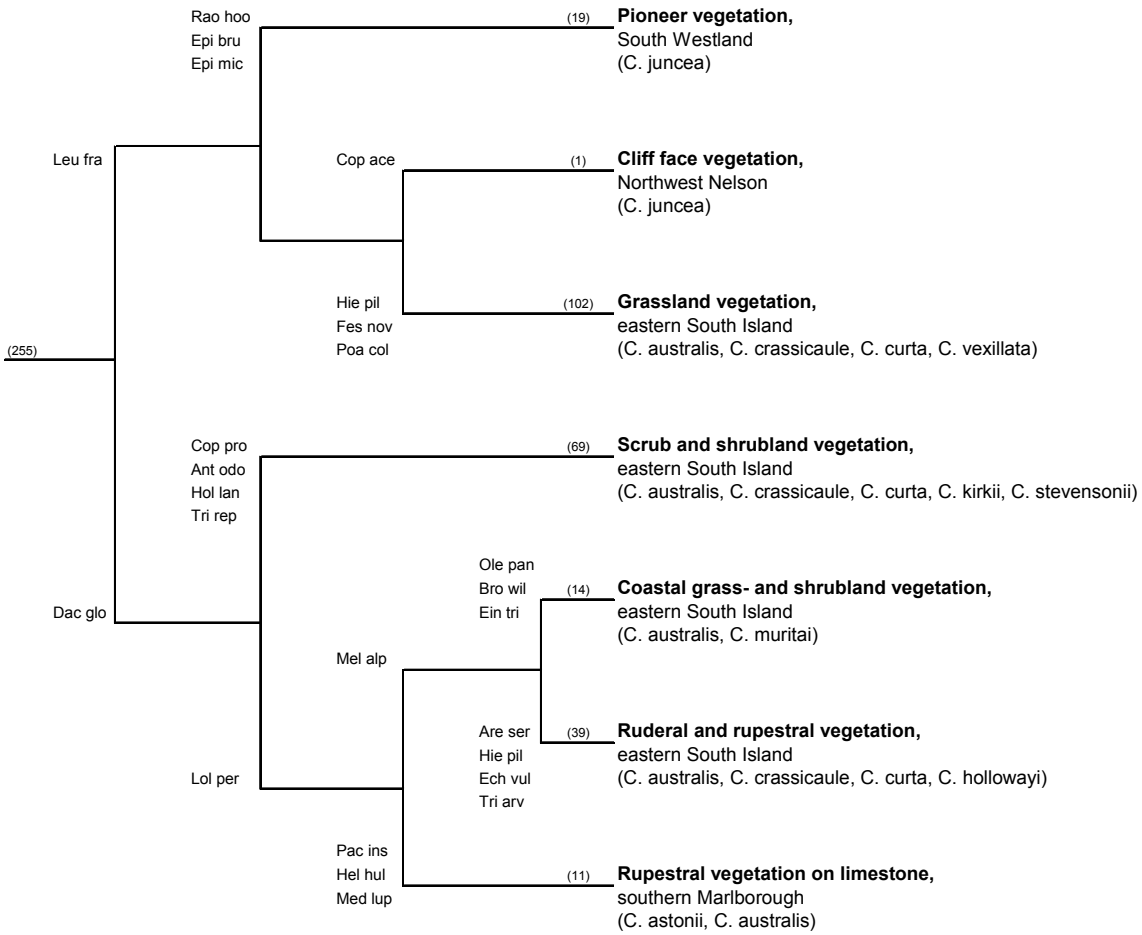


Fig. 4.1: Classification of the 255 vegetation plots into seven main vegetation types. Indicator species are shown next to the branches for each division. The names are abbreviations of the binomial species names; see text and Table 4.2 -Table 4.14 for full names. Numbers in brackets indicate the number of plots in each type. The *Carmichaelia* species present in each vegetation type are listed.

Scrub and shrubland vegetation were characterised by the presence of the shrub *Coprosma propinqua* together with the herbs *Anthoxanthum odoratum, Holcus lanatus,* and *Trifolium repens*. This vegetation type mainly comprised plots sampled in vegetation with a tiered structure. Separated from this type was a group of plots representing coastal grass- and shrubland vegetation with the coastal shrub *Olearia paniculata* as well as *Bromus willdenowii* and *Einadia triandra* as indicator species. *Arenaria* serpyllifolia, *Hieracium pilosella*, *Echium vulgare,* and *Trifolium arvense* characterised ruderal and rupestral vegetation in the eastern South Island, while rupestral vegetation on Marlborough limestone was separated from this type by the presence of *Pachystegia insignis*, *Heliohebe hulkeana,* and *Medicago lupulina*.

In the second step of the analysis, each of the main vegetation types was divided into a number of distinct plant communities. A fold-out overview over these communities is provided in Appendix 2. The various *Carmichaelia* species differed notably in their occurrence in the vegetation types and plant communities, indicating distinct ecological differences between the species (Table 4.1).

Table 4.1: Distribution of the plots sampled for the *Carmichaelia* species relative to the main vegetation types and plant communities. Community numbers correspond with the section headings (see also fold-out overview in Appendix 2). ast – *C. astonii*, aus – *C. australis*, cra – *C. crassicaule*, cur – *C. curta*, hol - *C. hollowayi*, jun – *C. juncea*, kir – *C. kirkii*, mur – *C. muritai*, ste – *C. stevensonii*, vex – *C. vexillata*, * - regeneration observed in plots.

Vegetation type	Com.	ast	aus	cra	cur	hol	jun	kir	mur	ste	vex
Pioneer	4.4.1.1	.	.	.	.	.	8 *	.	.	.	.
	4.4.1.2	.	.	.	.	.	11 *	.	.	.	.
Cliff face	4.4.2	.	.	.	.	.	1	.	.	.	.
Grassland	4.4.3.1	.	.	1	.	.	.	.	.	.	7
	4.4.3.2	.	8 *	6 *	4 *	.	.	.	.	.	18 *
	4.4.3.3	.	3 *	37 *	.	.	.	.	.	.	18 *
	4.4.3.4	.	.	7 *	.	.	.	.	.	.	.
Scrub and shrubland	4.4.4.1	.	2 *	.	.	.	.	2 *	.	.	.
	4.4.4.2	.	6 *	.	.	.	.	.	.	.	.
	4.4.4.3	.	4 *	.	.	.	.	1 *	.	8 *	.
	4.4.4.4	.	10 *	.	.	.	.	4 *	.	.	.
	4.4.4.5	.	5 *	4	1	.	.	26 *	.	.	.
	4.4.4.6	.	1	.	.	.	.	3 *	.	.	.
Coastal grass- and shrubland	4.4.5.1	.	4	.	.	.	.	.	4	.	.
	4.4.5.2	.	6	.	.	.	.	.	.	.	.
	4.4.5.3	.	2	.	.	.	.	.	1	.	.
Ruderal and rupestral	4.4.6.1	.	1	.	.	8 *	.	.	.	.	.
	4.4.6.2	.	.	.	8 *	.	.	.	.	.	.
	4.4.6.3	.	.	.	10 *	.	.	.	.	.	.
	4.4.6.4	.	2	5 *	8 *	.	.	.	.	.	.
Marlb. limestone	4.4.7	10 *	6	.	.	.	.	.	.	.	.
Total no. of plots		10	60	60	31	8	20	36	5	10	43

While the plots sampled for *C. astonii*, *C. hollowayi*, and *C. stevensonii* were restricted to a single plant community each, all other species occurred in a range of communities. However, most species were restricted to one of the main vegetation types, and here, the plots appeared clustered in certain communities. For example, all plots of *C. kirkii* were grouped under scrub and shrubland with most plots representing community 4.4.4.5 (*Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland). Similarly, *C. vexillata* was only found in grassland communities, and the majority of plots was allocated to communities 4.4.3.2 (*Hieracium pilosella* herbfield) and 4.4.3.3 ((*Chionochloa* spp) – (*Hieracium pilosella*) tussock grassland). *C. muritai* was restricted to communities in coastal grass- and shrubland vegetation.

C. australis, *C. crassicaule*, *C. curta*, and *C. juncea* appeared more widespread, occurring in a range of communities belonging to several of the main vegetation types, but their plots also showed prominence in certain types and plant communities. *C. crassicaule* was mainly found in grassland vegetation with most of its plots representing community 4.4.3.3 ((*Chionochloa spp.*) – (*Hieracium pilosella*) tussock grassland). Similarly, *C. curta* occurred mainly in communities of ruderal and rupestral vegetation, while *C. juncea* was restricted to the pioneer and cliff face vegetation.

C. australis was the most widespread species occurring in all vegetation types except the pioneer and cliff face vegetation. However, the majority of its plots was allocated to the various scrub and shrubland communities, including coastal grass- and shrubland, while it was not found in several of the grassland and ruderal and rupestral communities.

Regeneration was observed for all *Carmichaelia* species, except *C. muritai*, and usually coincided with the plant communities where most of the plots of a species were grouped.

In the following sections, the plant communities identified within the seven main vegetation types were analysed to characterise the current habitats of the *Carmichaelia* species in more detail and to further clarify ecological similarities and differences between the species.

4.4.1 Pioneer Vegetation, South Westland

This vegetation type represented the present habitats of *C. juncea* at its three known locations in South Westland. Two of the populations are located at altitudes between 100 and 200 m in the lower Waiho and Fox Rivers. The third population can be found at Welcome Flat, an area of alluvial terraces in the Copland Valley at around 450 m a.s.l.. The recorded plant communities occurred on young surfaces in the active riverbed as well as on older terraces beside the rivers.

Two communities were distinguished correlating with the age of the surfaces. The [*Raoulia hookeri*] sand- or gravelfield occurred as a pioneer community on young surfaces, while the [*Raoulia hookeri*] – [*Holcus lanatus*] grassland occurred on older alluvial flats. Both communities were characterised by the presence of the small growing, pioneering herbs *Raoulia hookeri, R. tenuicaulis, Epilobium brunnescens,* and *E. microphyllum,* and the adventive grass *Agrostis capillaris* (Table 4.2). Juveniles of *C. juncea* were present in both communities.

Fig. 4.2: [*Raoulia hookeri*] sand- or gravelfield in habitat of *C. juncea* on a young alluvial surface in the lower Waiho River (GR: H35 800 555).

4.4.1.1 [*Raoulia hookeri*] sand- or gravelfield (8 plots)

The [*Raoulia hookeri*] sand- or gravelfield has been described by Wardle (1977, 1991) under the name '*Raoulia* community' as the typical pioneer community of lowland river flats below 200 m altitude in Westland. Consistent with this, the community was found on young alluvial surfaces in the two lowland populations of *C. juncea*, in the Waiho and Fox Rivers (Table 4.3). It was characterised by the basic set of pioneer species mentioned above, with only few additional species. Vegetation cover was sparse, with a relatively large cryptogam component (Fig. 4.2). In contrast to Wardle's description (1977) and observations by Norton et al. (1998), the plots recorded here showed *Raoulia hookeri* as the most frequent and dominant pioneer, while *R. tenuicaulis* occurred as a minor component. With 8 ± 1.2 species/plot, this community showed little diversity.

Fig. 4.3: [*Raoulia hookeri*] – [*Holcus lanatus*] grassland in habitat of *C. juncea* on an older alluvial surface at Welcome Flat (GR: H36 663 255).

4.4.1.2 [*Raoulia hookeri*] – [*Holcus lanatus*] grassland (11 plots)

The [*Raoulia hookeri*] – [*Holcus lanatus*] grassland represented a later successional stage in the development of alluvial surfaces (Wardle 1977). As it was present in all three populations of *C. juncea* in South Westland, its occurrence appeared not to be related to altitude (Table 4.3), but rather dependent on the age of the alluvial surface.

Introduced grasses and herbs were prominent, although the early pioneer species were still present. *Coprosma acerosa* and *Muehlenbeckia axillaris* represented indigenous elements typical of seral grassland communities (Wardle 1991). Total vegetation cover was comparatively dense, again with a strong cryptogam component (Fig. 4.3). With 18 ± 1.6 species/plot this community was distinctly more diverse than the [*Raoulia hookeri*] sand- or gravelfield.

Table 4.2: Pioneer vegetation on alluvial flats, South Westland, and cliff face community, Northwest Nelson in habitats of *C. juncea*. All species occurring with a frequency > 40% in at least one community are shown. % cover is mean cover over all plots in the community, ● - < 1% cover, + - frequency ≤ 40% in this community.

Community **4.4.**	**1.1**	**1.2**	**2**
No. of plots	8	11	1
No. of vascular plant species/plot	8	18	19
Standard error	1.2	1.6	/
Mean cover (%)			
Vascular plants	11	38	5
Moss and lichen	14	29	85
Litter	1	4	.
Bare ground	67	29	.
Rocks (> 20 cm)	8	5	95
Species (% cover)			
Carmichaelia juncea	1	8	1
Juveniles	+	1	.
Raoulia hookeri	8	9	.
Epilobium brunnescens	1	2	.
Epilobium microphyllum	2	1	.
Raoulia tenuicaulis	+	3	.
Agrostis capillaris	1	+	.
Holcus lanatus	●	7	.
Hypochoeris radicata	+	5	●
Hieracium praealtum	.	3	.
Anthoxanthum odoratum	+	3	.
Trifolium repens	.	3	.
Coprosma acerosa	.	1	●
Muehlenbeckia axillaris	.	2	.
Olearia avicenniifolia	.	2	●
Microtis unifolia	+	2	.
Gnaphalium audax	.	1	.
Lachnagrostis lyallii	+	●	.
Cassinia leptophylla	.	.	●
Celmisia 'pupu'	.	.	●
Colobanthus muelleri	.	.	●
Eryngium vesiculosum	.	.	●
Hebe elliptica	.	.	●
Lachnagrostis spp.	.	.	●
Leptinella calcarea	.	.	●
Lobelia anceps	.	.	●
Luzula banksiana	.	.	●
Pimelea urvilleana	.	.	●
Plantago triandra subsp. masoniae	.	.	●
Poa pusilla	.	.	●
Selliera radicans	.	.	●
Trisetum antarcticum	.	.	●
Wahlenbergia congesta	.	.	●
further species with ≤ 40% frequency in all communities			

4.4.1.1 [*Raoulia hookeri*] sand- or gravelfield

4.4.1.2 [*Raoulia hookeri*] – [*Holcus lanatus*] grassland

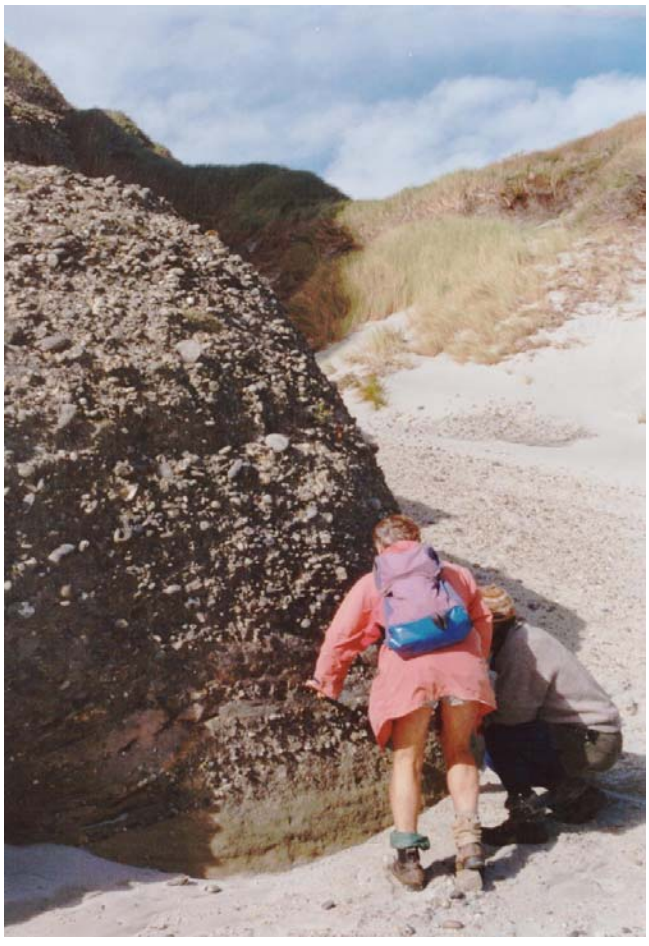
4.4.2 Cliff face community

Table 4.3: Altitude, slope, and aspect (± SE) associated with plant communities in pioneer and cliff face vegetation.

Community 4.4.	**1.1**	**1.2**	**2**
No. of plots	8	11	1
Altitude (m a.s.l.)	121 ± 9.4	336 ± 47.9	2
min	120	120	.
max	180	450	.
Slope (°)	0	0	45
min	.	.	.
max	.	.	.
Aspect (°)	.	.	180

4.4.2 Cliff Face Vegetation, Northwest Nelson (1 plot)

The cliff face vegetation was represented by a single plot sampled at the only known location of *C. juncea* in Northwest Nelson (Greenhills Stream). The plot included the whole population of currently eight plants located on a cliff face of conglomerate rock about 2 m above a sandy beach. Plants rooted in fine rock material and in cracks of the solid rock surface, which was densely covered with a mat of crustose and foliose lichen (85% cover; Table 4.2, Table 4.3, Fig. 4.4).



A

B

Fig. 4.4: A – Habitat of *C. juncea* at Greenhills Stream, Northwest Nelson (GR: M24 807 777). B - Plants root in finer rock material and in cracks of the rock surface.

Vascular plant cover was very sparse, although with a total of 19 species the community was relatively species-rich. Only a few species linked this community with the *C. juncea* communities of South Westland (*Hypochoeris radicata, Coprosma acerosa, Olearia avicenniifolia*). Instead, a range of typically coastal species (e.g., *Colobanthus muelleri, Eryngium vesiculosum, Pimelea urvilleana*) were present reflecting the exposed conditions of the cliff face habitat. Several species endemic to the area of Northwest Nelson, such as *Trisetum antarcticum, Leptinella calcarea,* and *Wahlenbergia congesta*, were also recorded.

4.4.3 Grassland Vegetation

The 102 vegetation plots characterised as grassland vegetation were sampled in Canterbury and Otago in habitats of *Carmichaelia australis*, *C. crassicaule*, *C. curta*, and *C. vexillata*.

Most grasslands in New Zealand represent induced vegetation on sites where the original forest cover has been destroyed (Wardle 1991; Mc Glone 2001). Since the arrival of humans in New Zealand, most forest areas have been burnt and cleared, and at least since European settlement forest regeneration has largely been prevented by farm management. Farming practices, with regular fires, oversowing, fertiliser application, and livestock grazing, as well as the impact of feral mammals have further led to modification and degradation of indigenous grassland communities (Cockayne 1928; Zotov 1938; Wardle 1991).

All plots recorded here, were located in areas presently or previously used for livestock grazing. The adventives *Agrostis capillaris, Hieracium pilosella, H. praealtum*, and *Rumex acetosella* were always present, their varying abundance reflecting varying degrees of modification and degradation. Four communities were distinguished, following a gradient of decreasing degradation from sand- and herbfield over tussock grassland to tussock-shrubland (Table 4.4; Fig. 4.5). This gradient was consistent with an increase in species-richness and complexity of the communities, associated with an increase in altitude (Table 4.5). The connection with altitude is caused by the fact that farming intensity usually decreases with increasing altitude (Connor 1965; Wardle 1991).

The four identified communities did not represent stable, idiosyncratic units with characteristic sets of indicator species. Instead, the species typical for one community usually occurred in all the richer, less degraded communities, emphasising the induced character of the communities and their developmental relationship caused by increasing levels of degradation (c.f. Connor 1965).

Table 4.4: Grassland vegetation of the eastern South Island in habitats of *C. australis*, *C. crassicaule*, *C. curta*, and *C. vexillata*. % cover is mean cover over all plots in the community/type, ● - < 1% cover, + - ≤ 40% frequency in the respective community/type.

Community **4.4.**	**3.1**	**3.2**			**3.3**		**3.4**
Type			a	b	c	d	
No. of plots	9	30	19	19	11	7	7
No. of vascular plant species	11	16	23	29	30	30	31
Standard error	1.2	0.9	1.4	1.7	1.6	1.4	3.0
Mean cover (%)							
Vascular plants	35	52	70	75	84	66	64
Moss and lichen	4	2	2	2	2	2	12
Litter	1	1	3	5	6	12	25
Bare soil	60	42	25	11	10	22	22
Rocks (> 20 cm)	3	5	3	12	2	2	1
Species (% cover)							
Carmichaelia australis	.	+	+	+	+	.	.
Juveniles	.	+	+	.	.	.	.
Carmichaelia crassicaule	+	+	1	2	1	2	1
Juveniles	.	+	+	●	+	+	+
Carmichaelia curta	.	+	.	.	.	.	.
Juveniles	.	+	.	.	.	.	.
Carmichaelia vexillata	●	2	+	+	+	●	.
Juveniles	.	+	.	.	.	+	.
Festuca rubra	7	+	.	+	+	.	.
Achillea millefolium	1	+	+	+	.	.	.
Festuca novae-zelandiae	+	5	6	10	12	8	2
Poa colensoi	+	3	4	4	4	3	3
Anthoxanthum odoratum	+	5	7	12	5	4	1
Leucopogon fraseri	+	2	4	2	3	3	+
Wahlenbergia albomarginata	.	1	2	2	2	2	3
Chionochloa spp.	.	.	10	+	21	35	6
Pimelea oreophila	.	+	●	●	2	2	1
Raoulia subsericea	.	+	3	2	5	3	2
Celmisia gracilenta	.	.	2	●	2	2	2
Aciphylla aurea	.	.	1	3	4	6	●
Hypochoeris radicata	1	+	2	2	2	2	2
Viola cunninghamii	.	.	+	+	1	1	1
Trifolium repens	+	+	●	5	2	+	+
Elymus solandri	+	1	+	2	+	+	.
Cerastium fontanum	.	+	+	1	+	+	.
Acaena caesiiglauca	.	.	+	2	+	+	+
Crepis capillaris	+	+	.	●	.	.	.
Trifolium arvense	3	+	+	1	.	.	.
Brachyglottis bellidioides	.	+	+	+	2	●	3
Luzula rufa	+	.	+	+	2	+	1
Epilobium alsinoides	.	+	+	+	1	+	1
Helichrysum bellidioides	.	.	.	+	1	1	2
Gaultheria depressa	.	.	.	.	+	1	+
Gaultheria crassa	.	.	.	.	+	5	9
Leucopogon colensoi	.	.	+	+	+	4	●
Anisotome aromatica	.	.	.	+	.	2	3
Blechnum penna-marina	.	.	.	+	+	1	2
Dracophyllum uniflorum	.	.	.	.	.	.	3
Pimelea traversii	.	.	+	.	.	+	●
Hebe pinguifolia	.	.	.	.	.	.	●
Coprosma propinqua	.	.	.	+	.	.	●
Celmisia spectabilis	.	.	.	.	.	.	3
Kelleria dieffenbachii	.	.	+	.	+	.	1
Schizeilema hydrocotyloides	.	.	.	.	.	.	1
Ourisia caespitosa	.	.	.	.	.	.	●
Gingidia filifolia	.	.	.	.	.	.	●
Ranunculus insignis	.	.	.	.	.	.	●
Agrostis capillaris	9	4	14	13	8	9	3
Hieracium pilosella	8	29	22	8	15	5	+
Rumex acetosella	3	3	●	2	2	2	.
Hieracium praealtum	2	+	5	+	+	2	2
Discaria toumatou	+	+	4	8	5	4	+
Helichrysum filifolium	.	.	1	1	+	+	.
Geranium sessiliflorum	+	+	+	●	+	+	+
Carex breviculmis	+	+	+	1	1	+	.
Coprosma petrii	.	+	+	+	3	.	.
Ranunculus multiscapus	.	+	+	+	1	+	.
Craspedia lanata	.	+	.	+	+	1	.
Brachyscome longiscapa	.	.	.	+	+	1	.
Luzula banksiana	.	.	+	+	+	1	+
Thelymitra longifolia	.	+	+	+	+	●	.
Prasophyllum colensoi	.	+	+	+	+	●	.
Epilobium glabellum	.	.	+	.	.	●	.
Hieracium lepidulum	.	.	+	+	+	●	1
Deyeuxia avenoides	.	.	+	+	+	+	2

further species with ≤ 40% frequency in all communities

4.4.3.1 [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield

4.4.3.2 *Hieracium pilosella* herbfield

4.4.3.3 (*Chionochloa spp.*) – (*Hieracium pilosella*) tussock grassland

- a Type with *Hieracium pilosella*
- b Type with *Acaena caesiiglauca*
- c Type with *Brachyglottis bellidioides*
- d Type with *Gaultheria crassa*

4.4.3.4 [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland

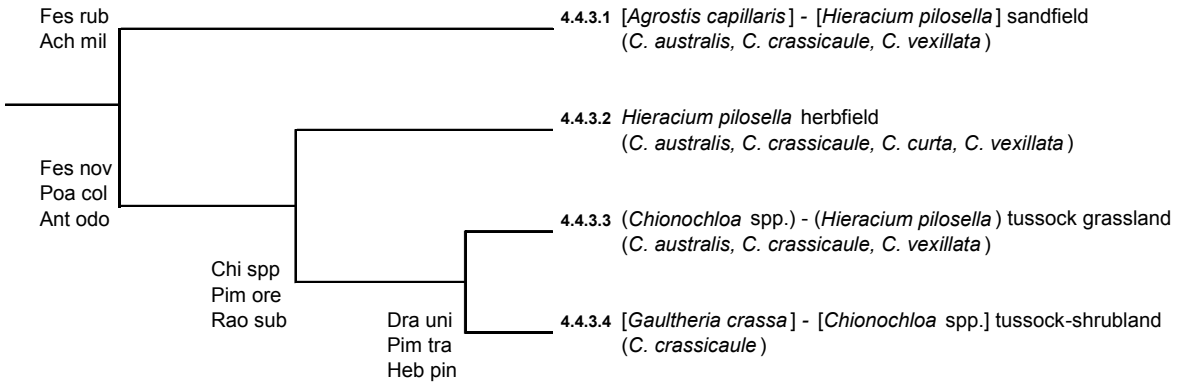


Fig. 4.5: Classification of grassland vegetation into four communities. Not all indicator species are shown (see Table 4.4 for complete list and full species names).

Table 4.5: Altitude, slope, and aspect (± SE) associated with plant communities in grassland vegetation.

Community 4.4.	**3.1**	**3.2**	**3.3a**	**3.3b**	**3.3c**	**3.3d**	**3.4**
No. of plots	9	30	19	19	11	7	7
Altitude (m a.s.l.)	504 ± 26.1	716 ± 32.7	857 ± 57.4	811 ± 41.7	886 ± 68.5	933 ± 88.0	937 ± 25.6
min	300	300	500	500	600	600	800
max	700	1200	1400	1300	1200	1300	1000
Slope (°)	15 ± 4.8	11 ± 1.9	14 ± 2.6	19 ± 3.8	18 ± 4.9	26 ± 7.4	23 ± 4.5
min	0	0	0	0	0	0	10
max	40	40	40	70	60	50	50
Aspect (°)	304 ± 19.4	359 ± 8.8	6 ± 17.9	87 ± 31.1	263 ± 24.1	40 ± 33.2	182 ± 13.6
from	SE	S	SW	all	all	all	E
to	NW	NE	E	aspects	aspects	aspects	SW

4.4.3.1 [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield (9 plots)

The [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield represented highly degraded grasslands in the Mackenzie Basin and its adjacent hill country. It was found in habitats of *C. crassicaule*, and *C. vexillata* at relatively low altitudes (300 - 700 m). Plots were located on terraces as well as slopes with gradients up to 40° and SE to NW aspects.

The vegetation cover was very sparse (35%) and dominated by *Agrostis capillaris*, *Hieracium pilosella*, and *Festuca rubra* (Fig. 4.6). Regularly associated were adventive herbs (*Achillea millefolium, Hypochoeris radicata, Trifolium repens, Rumex acetosella, Hieracium praealtum*), while species typical of indigenous grassland occurred only scattered in some of the plots. The community was very species-poor with 11 ± 1.2 species/plot. Regeneration of the *Carmichaelia* species was not observed.

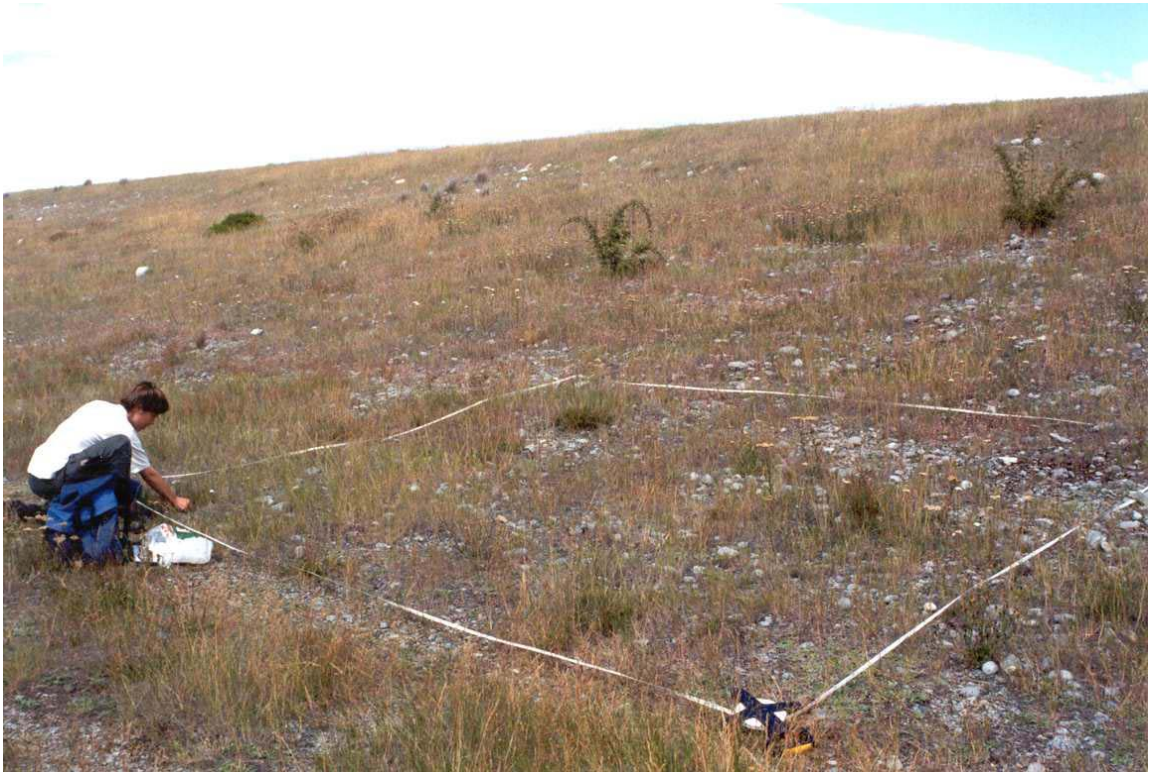


Fig. 4.6: [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield in habitat of *C. vexillata*, Pukaki-Ohau Canal, Mackenzie Basin (GR: H38 681 562).

4.4.3.2 *Hieracium pilosella* herbfield (30 plots)

The *Hieracium pilosella* herbfield was found as plant community in habitats of *C. australis*, *C. crassicaule*, *C. curta*, and *C. vexillata*. The plots were sampled in southern Canterbury and Central Otago over a wide range of altitudes (300 – 1200 m), although most plots were located between 600 and 900 m. Slopes were usually gentle, but reached gradients of over 30° in some plots, with mainly N and W aspects.

The *Hieracium pilosella* herbfield represented a community of degraded short tussock grassland, as the indicator species were species typical for this type of indigenous grassland (*Festuca novae-zelandiae, Poa colensoi, Leucopogon fraseri, Wahlenbergia albomarginata*; Wardle 1991). However, the invasive *Hieracium pilosella* was the most prominent species with almost 30% cover, reflecting the degraded state of the plant community (Fig. 4.7). Adventive grasses (*Agrostis capillaris*, *Anthoxanthum odoratum*) were also prominent, with similar cover to the native species.

Overall ground cover was relatively sparse, leaving 47% of bare soil and rocks exposed. With 16 ± 0.9 species/plot, the community was slightly more diverse than the [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield. Juvenile plants of the *Carmichaelia* species were present in some plots.

Fig. 4.7: *Hieracium pilosella* herbfield in habitat of *C. vexillata* in the Mackenzie Basin (GR: I37 043 827).

4.4.3.3 (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland

(*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland was found over a range of sites from southern Canterbury to Central Otago in habitats of *C. australis*, *C. vexillata*, and in particular, *C. crassicaule*. The plots were recorded at various altitudes (500 – 1400 m) on slopes with gradients up to 50° in all aspects.

The group of short tussock species characteristic of the previous community was present, and associated with a set of further species typical for indigenous grasslands (*Pimelea oreophila, Raoulia subsericea, Celmisia gracilenta, Aciphylla aurea, Viola cunninghamii*; Wardle 1991). The presence of snow tussocks (*Chionochloa* species) characterised these stands as snow tussock grasslands, although, depending on the degree of modification of the sites, they were not always prominent. Within this community, four types were distinguished, correlating with the degree of degradation.

4.4.3.3 a Type with *Hieracium pilosella* (19 plots)

This type of (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland was characterised by the dominance of *Hieracium pilosella*, indicating strong degradation of the sites. Adventive grasses were also prominent, while snow tussocks reached only 10% cover. The species-richness was relatively low, with 23 ± 1.4 species/plot. Juveniles of *C. australis* and

C. crassicaule were present in some of the plots, while regeneration of *C. vexillata* was not observed.

Fig. 4.8: (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland in its type with *Hieracium pilosella* in habitat of *C. vexillata*, at Lindis Pass (GR: G40 434 190).

4.4.3.3 b Type with *Acaena caesiiglauca* (19 plots)

Species composition and abundance characterised the type with *Acaena caesiiglauca* as slightly less modified compared to the type with *Hieracium pilosella*. Although the vegetation was dominated by adventive grasses (*Anthoxanthum odoratum, Agrostis capillaris*) and *Hieracium pilosella* was still prominent, the relatively high cover of *Festuca novae-zelandiae* and the presence of *Acaena caesiiglauca*, together with increased species-richness (29 ± 1.7 species/plot), pointed towards more intact grassland communities (c.f. Moore 1976; Scott et al. 1988). *Chionochloa* species were only infrequently present, but the other species found to be characteristic of snow tussock grassland in this study were abundant. The sites were relatively rocky, which was reflected by the presence of species typical for dry and open sites (*Elymus solandri, Crepis capillaris, Trifolium arvense*) as well as by higher cover of *Discaria toumatou*. Plots with *C. crassicaule* usually showed regeneration of this species, while *C. australis* and *C. vexillata* were only observed as adult plants.

4.4.3.3 c Type with *Brachyglottis bellidioides* (11 plots)

The vegetation in this type was dense and dominated by tussocks of *Chionochloa* species and *Festuca novae-zealandiae* (Fig. 4.9). Small native herbs and creepers, like *Brachyglottis bellidioides* or *Gaultheria depressa*, were abundant, and often found at the base of the snow tussocks or amongst *Aciphylla aurea*. Although *Hieracium pilosella* and adventive grasses were relatively prominent, the dominance of the native tussocks and abundance of native herbs indicated comparatively low degradation of this community type. Species-richness was high with 30 ± 1.6 species/plot. Similar to the previous type, juveniles of *C. crassicaule* were present in some of the plots, while regeneration of *C. australis* and *C. vexillata* was not observed.

Fig. 4.9: (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland in its type with *Brachyglottis bellidioides* in habitat of *C. crassicaule*, Long Gully, Central Otago (GR: H41 708 834).

4.4.3.3 d Type with *Gaultheria crassa* (7 plots)

The type with *Gaultheria crassa* was only recorded in habitats of *C. crassicaule* and *C. vexillata*. It appeared as the least modified type of snow tussock grassland in this study. *Chionochloa* species were clearly dominant, and the set of native species typical for the previous type was supplemented by the small shrubs *Leucopogon colensoi* and *Gaultheria crassa*, as well as *Anisotome aromatica* and *Blechnum penna-marina*. In addition, a range of other native herbs occurred with increased frequency (*Craspedia lanata, Brachyscome longiscapa, Luzula banksiana, Thelymitra longifolia, Prasophyllum colensoi, Epilobium glabellum*). Adventive herbs and grasses were still present, but the cover of *Hieracium pilosella* was clearly reduced. The type was species-rich with 30 ± 1.4 species/plot. Notable

was the relatively open vegetation cover in this type and the higher cover of litter on the ground. These features together with the presence of the shrubs suggested a connection to the following community. Regeneration of both *Carmichaelia* species, *C. crassicaule* and *C. vexillata*, was observed.

4.4.3.4 [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland (7 plots)

The [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland was only recorded in habitats of *C. crassicaule* at relatively high altitudes in Mid Canterbury (800 – 1000 m). The sites were located on slopes with 10 – 50° gradients and E to SW aspects.

The community appeared to represent secondary shrubland regenerating on sites where beech forest had been removed by fire, as it showed the characteristic combination of tussock grassland species and shrubs of subalpine heaths typical for such secondary communities (Wardle 1991; see also Molloy 1963).

Vascular plant cover was relatively open, but as mosses and lichens were abundant and a litter layer developed, only 23% of bare ground and rocks were left exposed. The vegetation appeared as a mosaic of the species present, with none being actually dominant. *Gaultheria crassa*, the *Chionochloa* tussocks, and *Dracophyllum uniflorum*, as typical heath species, were the most conspicuous (Fig. 4.10). The occurrence of adventives was greatly reduced in this community, and species-richness was high with 31 ± 3.0 species/plot. Juveniles of *C. crassicaule* were present in some of the plots.

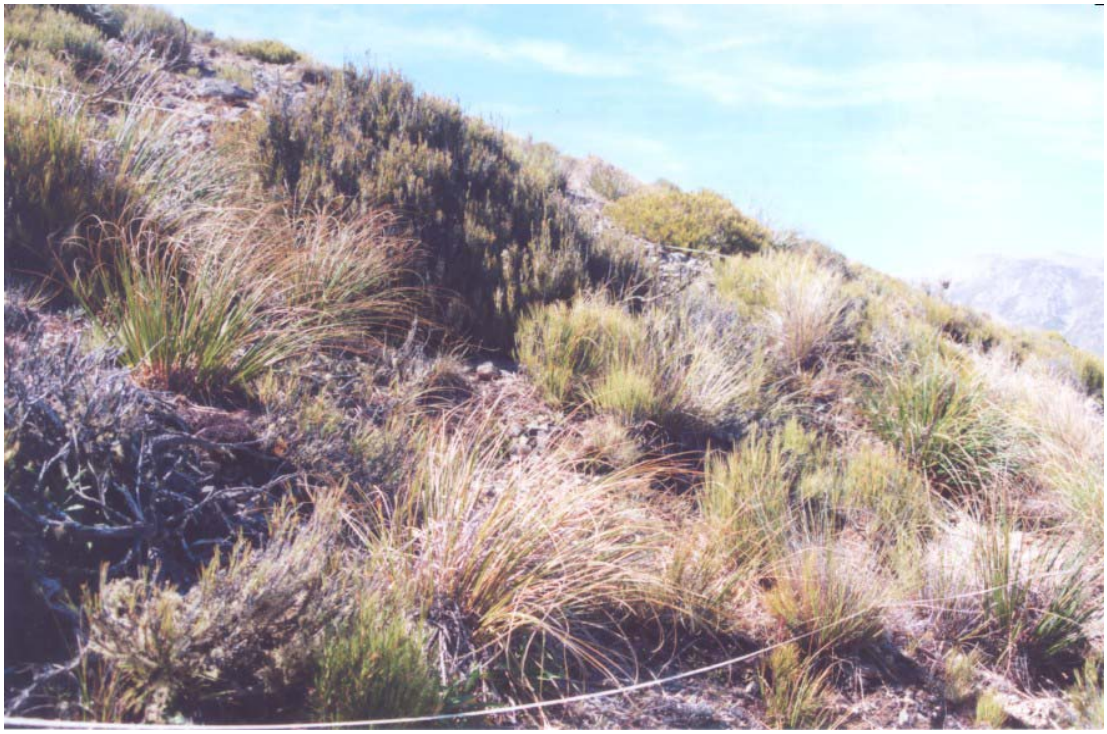


Fig. 4.10: [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland in habitat of *C. crassicaule*, Porters Pass, Canterbury (GR: K35 080 672).

4.4.4 Scrub and Shrubland Vegetation

Scrub and shrubland vegetation was represented by 69 plots sampled in the east of the South Island from southern Marlborough to Central Otago, in populations of *C. australis*, *C. crassicaule, C. curta, C. kirkii*, and *C. stevensonii*. The vegetation was characterised by a more complex structure, with one or two shrub layers above the ground layer (Table 4.6, Table 4.8). As mean top height did not exceed 7 m and trees with a stem diameter > 10 cm were rarely present, the communities were classed as scrub and shrubland vegetation rather than forest (Atkinson 1985).

The shrub *Coprosma propinqua* was always present, together with a range of adventive grasses and herbs (*Dactylis glomerata, Holcus lanatus, Cerastium fontanum, Trifolium repens, Crepis capillaris, Hieracium pilosella*) indicating relatively open and fertile conditions.

Six communities were distinguished (Fig. 4.11). The first three represented scrub and shrubland communities of the southern Marlborough region, separated from the other communities by the presence of two Marlborough endemics, *Brachyglottis monroi* and *Hebe traversii*, as well as the pioneer shrub *Cassinia leptophylla* and *Mycelis muralis*.

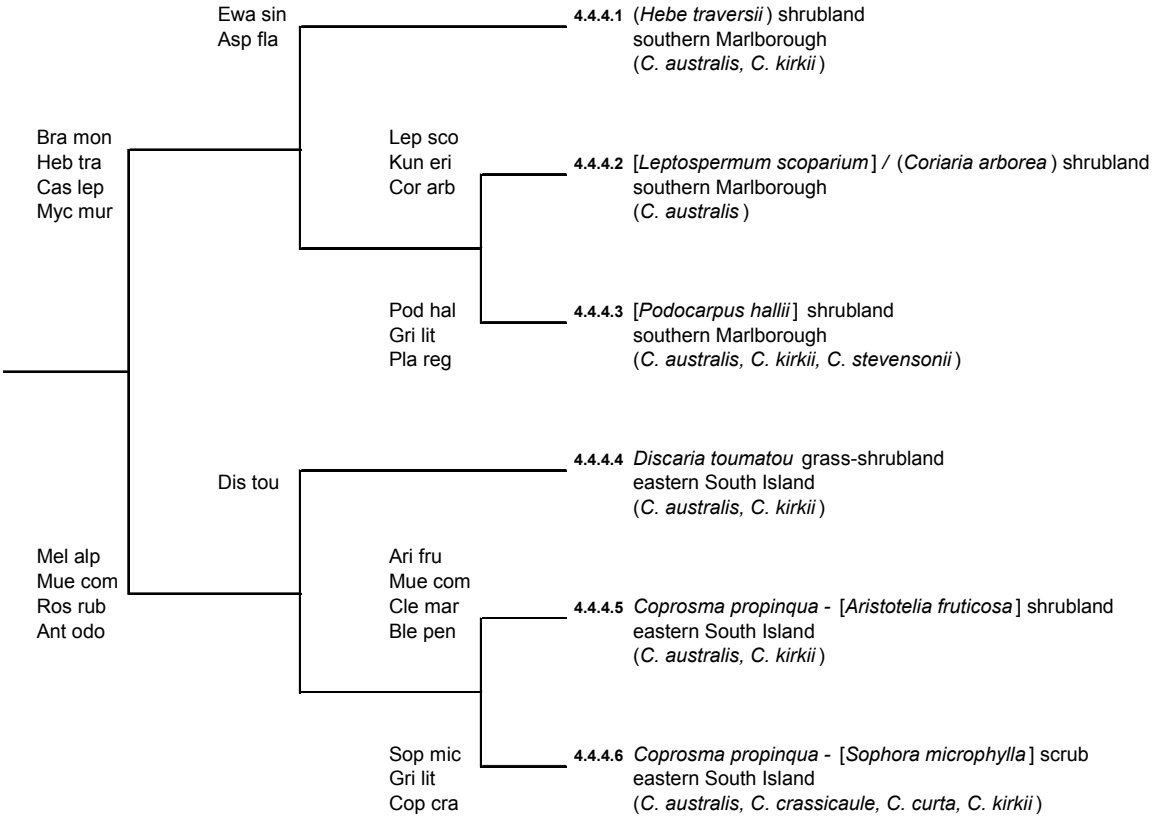


Fig. 4.11: Classification of scrub and shrubland vegetation into six communities. Not all indicator species are shown; see Table 4.6 and Table 4.8 for complete list of indicators and full species names.

Communities 4.4.4.4 to 4.4.4.6 were distinct due to the presence of *Melicytus alpinus, Muehlenbeckia complexa, Rosa rubiginosa* and *Anthoxanthum odoratum*. They comprised plots sampled along the east of the South Island from Marlborough to Otago, and represented shrubland types often described as ‘grey scrub', which is characterised by the prominence of divaricate (filiramulate) shrubs and climbers (Wardle 1991).

4.4.4.1 (*Hebe traversii*) shrubland (4 plots)

The (*Hebe traversii*) shrubland was found in habitats of *Carmichaelia australis* and *C. kirkii* in the area of the Tone Valley, Inland Kaikoura Ranges, at altitudes between 1000 and 1100 m (Table 4.7). Plots were located on steep rocky faces (30-70°) above the river with aspects ranging from NE to SW.

The community was characterised by a relatively dense shrub layer with a mean top height of 1.7 ± 0.2 m (Table 4.6; Fig. 4.12). *Brachyglottis monroi* and *Hebe traversii* were constantly present, the latter being the most prominent. Other notable shrub species included *Olearia nummulariifolia* and *Aristotelia fruticosa.* Where present, *Carmichaelia kirkii* was prominent reaching 15% cover in one of the plots. The ground layer was sparse, with *Hieracium pilosella* being the most prominent species. Two rupestral species, *Ewartia sinclairii* and *Asplenium flabellifolium*, were consistently present and characterised the (*Hebe traversii*) shrubland in this study. They were further associated with a varying combination of species characteristic of open and dry or rupestral habitats (e.g., *Muehlenbeckia axillaris*, *Helichrysum intermedium, Rytidosperma setifolium, Stellaria gracilenta, Asplenium trichomanes*). The overall species-richness was relatively low (25 ± 4.1 species/plot). Juveniles of the two *Carmichaelia* species were observed.

The (*Hebe traversii*) shrubland recorded here corresponded with the ‘*Brachyglottis monroi* - (*Hebe* spp.) scrub’ described by Williams (1989) as seral scrub community of precipitous slopes and unstable sites in the area of the Inland Kaikoura Ranges. In contrast to his description, shrub cover in the stands recorded here, was less than 80% and *Brachyglottis monroi* only a minor component. However, Williams (1989) also mentions a more open type of the community, characterised by the presence of rupestral species, as was found in this study. *Carmichaelia carmichaeliae,* recorded by Williams (1989) as usually present, was not observed in the area of the Tone Valley.

Fig. 4.12: (*Hebe traversii*) shrubland in habitat of *C. kirkii*, Tone Valley (GR: O30 429 999).

The following two communities were related to the (*Hebe traversii*) shrubland, as *Brachyglottis monroi* and *Hebe traversii* were frequently present. However, both species were usually minor components, while later successional species were more prominent, indicating that these communities represented later successional vegetation typical of more stable sites.

4.4.4.2 [*Leptospermum scoparium*] / (*Coriaria arborea*) shrubland (6 plots)

This community was represented by six plots sampled for *C. australis* in the coastal ranges of southern Marlborough at relatively low altitudes (300 - 700 m). Plots were located in streamside habitats on rocky terraces as well as steep banks with aspects varying from NW to SE.

A range of pioneer and short-lived shrubs and trees formed an open shrub tier, characterising this community as seral shrubland (Fig. 4.13). *Leptospermum scoparium* was dominant, accompanied by *Coprosma propinqua*, *Kunzea ericoides*, and *Coriaria arborea*. *Carmichaelia australis* formed a prominent component in all recorded stands. They reached mean top heights of 4.7 ± 1.4 m. The ground layer was dominated by *Coriaria arborea*, together with young plants of *Brachyglottis monroi*. Non-woody species were mainly grasses and herbs characteristic of relatively open and fertile conditions (*Poa cita*, *Dactylis glomerata,*

Holcus lanatus, Medicago lupulina, Hieracium pilosella). The community was species-rich with 32 ± 2.7 species/plot. Juveniles of *C. australis* were observed in some of the plots.

Fig. 4.13: [*Leptospermum scoparium*] / (*Coriaria arborea*) shrubland in habitat of *C. australis*, Hapuku River, Kaikoura (GR: O31 634 813).

Leptospermum scoparium shrublands and related communities have been described from streamside habitats in the area of the Inland and Seaward Kaikoura Ranges by Wardle (1971; 'kanuka scrub'), Williams (1989; '*Kunzea ericoides* - (*Leptospermum scoparium*) scrub'), and Druce and Williams (1989; '*Leptospermum scoparium* - *Cassinia* shrubland'). *Leptospermum scoparium* or *Kunzea ericoides* are the prominent shrubs in all these communities, associated with other pioneer species. The exact species composition and abundance/dominance relationships vary with local site conditions.

Table 4.6: Shrubland vegetation of southern Marlborough in habitats of *C. australis*, *C. kirkii*, and *C. stevensonii*. All species occurring with a frequency > 40% in at least one community are shown. % cover is the total cover of the species over all tiers averaged over all plots in the community/type, ● - < 1% cover, + - frequency ≤ 40% in this community.

Community	**4.4.**	**4.1**	**4.2**	**4.3**	
Type				a	b
No. of plots		4	6	5	4
No. of vascular plant species		25	32	36	35
Standard error		4.1	2.7	4.6	2.1
Top height		1.7	4.7	5.2	5.8
Standard error		0.2	1.4	0.7	0.3
Mean cover (%)					
Upper shrub tier		.	44	58	26
Lower shrub tier		63	.	.	38
Ground tier		23	43	38	51
Moss and lichen		2	2	1	2
Litter		14	24	33	2
Bare ground		10	20	24	17
Rocks (> 20 cm)		20	29	2	1
Species (% cover)					
Carmichaelia australis		4	4	2	.
Juveniles		+	+	+	.
Carmichaelia kirkii		8	.	+	.
Juveniles		●	.	+	.
Carmichaelia stevensonii		.	.	11	5
Juveniles		.	.	.	1
Ewartia sinclairii		●	.	.	.
Asplenium flabellifolium		1	+	+	.
Leptospermum scoparium		.	5	.	.
Kunzea ericoides		.	3	.	.
Olearia paniculata		.	●	.	.
Sophora microphylla		.	●	.	.
Coriaria arborea		.	11	.	.
Coprosma linariifolia		.	●	.	.
Coprosma rubra		.	●	.	.
Echium vulgare		+	1	+	.
Polystichum richardii		.	●	.	+
Phymatosorus diversifolius		.	2	.	.
Podocarpus hallii		.	+	8	8
Griselinia littoralis		.	+	2	4
Plagianthus regius		.	.	+	2
Phormium tenax		+	+	1	4
Viola cunninghamii		.	.	2	3
Epilobium wilsonii		.	.	2	2
Trifolium repens		.	+	1	3
Phyllocladus alpinus		+	.	9	.
Olearia nummulariifolia		8	+	6	.
Olearia coriacea		.	.	5	.
Pseudopanax colensoi		.	.	4	.
Dracophyllum acerosum		.	.	●	.
Coriaria sarmentosa		.	.	2	.
Chionochloa spp.		.	+	5	.
Gingidia montana		.	+	2	.
Gingidia trifoliolata		.	.	1	.
Celmisia monroi		.	+	1	.
Blechnum penna-marina		+	+	2	.
Polystichum vestitum		.	+	+	11
Poa cita		+	4	+	5
Festuca multinodis		.	.	.	5
Elymus solandri		●	2	.	2
Lolium perenne		.	.	.	2
Trisetum lepidum		.	.	.	●
Bulbinella angustifolia		.	.	.	6
Ranunculus reflexus		.	+	.	3
Hydrocotyle novae-zeelandiae		.	.	+	3
Medicago lupulina		.	2	.	2
Crepis capillaris		+	2	.	2
Galium aparine		.	.	.	2
Cardamine debilis		.	+	.	1
Digitalis purpurea		.	.	.	●
Geranium microphyllum		.	+	+	●
Brachyglottis monroi		4	3	6	.
Hebe traversii		17	2	14	●
Cassinia leptophylla		●	+	+	4
Mycelis muralis		+	1	1	3
Coprosma propinqua		●	4	1	10
Dactylis glomerata		2	3	2	12
Cerastium fontanum		2	●	+	3
Holcus lanatus		.	2	2	3
Hieracium pilosella		5	2	+	.
Aristotelia fruticosa		8	.	+	+
Rosa rubiginosa		●	.	+	.
Muehlenbeckia axillaris		4	+	.	.
Festuca novae-zelandiae		2	.	.	.
Rumex acetosella		2	+	+	.
Hieracium lepidulum		2	+	1	.
Hieracium caespitosum		2	.	+	.
Stellaria gracilenta		2	.	.	+
Asplenium trichomanes		2	.	.	.
Hebe spp.		1	.	+	.
Discaria toumatou		1	.	+	●
Gingidia filifolia		●	.	●	+
Coprosma spp.		●	.	.	.
Rytidosperma setifolium		●	.	.	.
Helichrysum intermedium		●	.	.	.
Luzula spp.		●	.	+	.
Celmisia spp.		●	.	+	.
Clematis forsteri		+	.	1	+
Hypochoeris radicata		.	+	1	+

further species with ≤ 40% frequency in all communities

4.4.4.1 (*Hebe traversii*) shrubland

4.4.4.2 [*Leptospermum scoparium*] / (*Coriaria arborea*) shrubland

4.4.4.3 [*Podocarpus hallii*] shrubland

a Type with *Phyllocladus alpinus*

b Type with *Polystichum vestitum*

Table 4.7: Altitude, slope, and aspect (± SE) associated with shrubland communities of southern Marlborough.

Community 4.4.	**4.1**	**4.2**	**4.3a**	**4.3b**
No. of plots	4	6	5	4
Altitude (m a.s.l.)	1030 ± 20.0	497 ± 74.9	1044 ± 34.9	1005 ± 5.8
min	1000	300	1000	1000
max	1100	700	1200	1100
Slope (°)	49 ± 8.2	26 ± 11.4	36 ± 6.4	45 ± 5.8
min	30	0	20	30
max	70	80	50	60
Aspect (°)	124 ± 32.9	343 ± 28.8	48 ± 30.2	60 ± 8.0
from	NE	NW	NW	NE
to	SW	SE	SE	E

4.4.4.3 [*Podocarpus hallii*] shrubland

[*Podocarpus hallii*] shrubland was found in habitats of *C. australis*, *C. kirkii*, and *C. stevensonii* in the area of the Inland and Seaward Kaikoura Ranges. Plots were sampled at relatively high altitudes (1000-1200 m) on steep slopes (20-60°) with aspects ranging from NW to SE.

In this community, the elements of the (*Hebe traversii*) shrubland were associated with forest species (*Podocarpus hallii, Griselinia littoralis, Plagianthus regius*), forming relatively tall stands of shrubland vegetation (5.4 ± 0.4 m). *Phormium tenax*, *Viola cunninghamii, Epilobium wilsonii*, and *Trifolium repens* were distinctive species in the ground layer. With 36 ± 2.4 species/plot, the [*Podocarpus hallii*] shrubland was the richest scrub and shrubland community described in this study.

This shrubland was related to the ‘podocarp scrub’ communities and ‘podocarp woodland’ described by Wardle (1971) and Williams (1989) for the area of the Inland and Seaward Kaikoura Ranges. Wardle (1991) pulls these and similar communities of the eastern South Island together as ‘*Griselinia littoralis* bush’, a group of induced scrub and forest communities characterised by the presence of remnant or re-established podocarps with prominence of broad-leaved trees. The exact species composition in these communities varies considerably depending on altitude, local habitat conditions, and the history of modification (Wardle 1991). The stands described in this study could be remnants of formerly more extensive forest or scrub stands, or they might have re-established through succession after a major disturbance event. Two types of [*Podocarpus hallii*] shrubland were distinguished.

4.4.4.3 a Type with *Phyllocladus alpinus* (5 plots)

The [*Podocarpus hallii*] shrubland in a type with *Phyllocladus alpinus* was recorded from a *Carmichaelia stevensonii* population at George Stream, Seaward Kaikoura Ranges, as well as from sites with *C. kirkii* in the Tone Valley, Inland Kaikoura Ranges.

Hebe traversii was the dominant shrub in this type, highlighting the connection with earlier successional communities. *Podocarpus hallii* was prominent and associated with a number of small trees and shrubs typical for subalpine scrub vegetation (*Phyllocladus alpinus, Olearia nummulariifolia, O. coriacea, Pseudopanax colensoi, Dracophyllum acerosum*). Where it occurred, *C. stevensonii* formed a prominent component in the shrub layer (Fig. 4.14). The ground vegetation was relatively sparse and dominated by young plants of the trees and shrubs as well as *Chionochloa* species. Juveniles of *C. australis* and *C. kirkii* were present in some of the plots. Mosses and lichens were sparse, but a relatively dense litter layer was developed, leaving only 24% of bare ground exposed.

Fig. 4.14: [*Podocarpus hallii*] shrubland in its type with *Phyllocladus alpinus* in habitat of *C. stevensonii*, George Stream, Seaward Kaikoura Ranges (GR: P30 723 999).

Similar scrub communities have been described by Druce and Williams (1989) and Williams (1989) for very steep slopes in the least modified areas of the Kaikoura Ranges. Consistent with this, the plant community described here, was found at fairly remote locations and in

relatively unmodified surroundings, on slopes with gradients up to 60°. The presence of species like *Gingidia montana* and *G. trifoliolata* indicated that browsing pressure in the community was low (Wardle 1991). Introduced species were sparse.

4.4.4.3 b Type with *Polystichum vestitum (4 plots)*

[*Podocarpus hallii*] shrubland in a type with *Polystichum vestitum* was represented by four plots sampled in a *Carmichaelia stevensonii* population at Mt Alexander, Seaward Kaikoura Ranges.

Podocarpus hallii, Griselinia littoralis, and *C. stevensonii* formed a sparse canopy above an open lower shrub tier dominated by *Coprosma propinqua*, young plants of *Podocarpus hallii*, and tall growing *Polystichum vestitum* (Fig. 4.15). The ground vegetation was comparatively dense and dominated by *Dactylis glomerata* and other adventive and native grasses, indicating relatively strong modification of the area. A range of species in the ground layer (*Poa cita, Bulbinella angustifolia, Ranunculus reflexus, Hydrocotyle novae-zelandiae, Medicago lupulina, Galium aparine, Cardamine debilis*) as well as the abundance of *Polystichum vestitum* indicated fertile and moist site conditions. This could be related to the fact that the eastern slopes of the Kaikoura ranges are subject to frequent coastal fogs providing extra moisture for the vegetation (Wardle 1971; Norton and Courtney 2000). Juveniles of *C. stevensonii* were present in three of the four plots.

The [*Podocarpus hallii*] shrubland in its Type with *Polystichum vestitum* is likely to represent a secondary scrub community on sites of former *Podocarpus hallii* forest. Williams (1982) describes this relationship for a similar community (*Cassinia leptophylla – Coprosma – Polystichum vestitum* scrub) in the Isolated Hill area. The *C. stevensonii* population at Mt Alexander is located in farming country and was subject to fires, oversowing, and livestock grazing in the past. The area is now protected, and the two tiered structure of the community could indicate regeneration of the formerly denser canopy in these stands.

Fig. 4.15: [*Podocarpus hallii*] shrubland in its type with *Polystichum vestitum* in habitat of *C. stevensonii*, Mt Alexander, Seaward Kaikoura Ranges (GR: P30 754 905).

Table 4.8: Shrubland vegetation of the eastern South Island ('grey scrub') with *C. australis*, *C. crassicaule*, *C. curta*, and *C. kirkii*. All species occurring with a frequency > 40% in at least one community are shown. % cover gives the total cover of the species over all tiers averaged over all plots in the community/type, ● - < 1% cover, + - frequency ≤ 40% in this community/type, cover values in brackets refer to individual plots in the community.

Community	**4.4.**	**4.4**	**4.5**			**4.6**
Type			a	b	c	
No. of plots		14	15	7	9	5
No. of vascular plant species		24	33	30	28	30
Standard error		2.5	2.4	0.9	1.5	2.8
Top height		2.3	3.0	2.4	2.5	6.4
Standard error		0.5	0.4	0.4	0.4	1.5
Mean cover (%)						
Upper shrub tier		(15)	(38)	.	.	50
Lower shrub tier		67	81	54	71	58
Ground tier		60	45	53	14	41
Moss and lichen		2	2	8	1	19
Litter		18	26	26	39	28
Bare ground		10	19	8	7	18
Rocks (> 20 cm)		6	6	14	46	3
Species (% cover)						
Carmichaelia australis		7	+	8	.	+
Juveniles		+	+	+	.	.
Carmichaelia crassicaule		.	.	.	●	.
Juveniles		.	.	.	.	.
Carmichaelia curta		.	.	.	+	.
Juveniles		.	.	.	.	.
Carmichaelia kirkii		+	11	7	5	3
Juveniles		+	●	●	●	+
Discaria toumatou		23	9	+	+	+
Aristotelia fruticosa		.	11	5	10	.
Muehlenbeckia complexa		2	12	3	8	+
Clematis marata		.	●	2	2	.
Blechnum penna-marina		.	5	+	2	+
Sophora microphylla		.	.	.	.	4
Griselinia littoralis		.	+	.	.	4
Coprosma propinqua x robusta		.	+	.	.	4
Coprosma crassifolia		.	.	.	.	●
Scandia geniculata		+	+	.	.	2
Muehlenbeckia australis		+	+	.	.	1
Digitalis purpurea		.	+	+	.	4
Asplenium richardii		.	.	1	+	2
Asplenium flabellifolium		+	+	1	.	2
Rubus schmidelioides		+	3	.	+	+
Polystichum vestitum		+	4	.	.	+
Festuca rubra		+	4	+	.	+
Mycelis muralis		+	1	.	.	+
Poa cita		1	.	3	2	.
Festuca novae-zelandiae		+	+	2	2	.
Elymus solandri		+	+	2	2	.
Poa colensoi		.	.	+	2	.
Trisetum lepidum		+	+	+	2	.
Acaena caesiiglauca		+	+	2	2	.
Wahlenbergia albomarginata		+	.	●	●	.
Rumex acetosella		+	+	2	●	.
Podocarpus hallii		.	.	.	17	.
Viola cunninghamii		+	+	.	●	.
Aciphylla aurea		.	.	+	2	.
Uncinia fuscovaginata		.	.	+	1	.
Arenaria serpyllifolia		.	+	.	●	.
Coprosma propinqua		4	29	15	30	21
Melicytus alpinus		+	2	4	6	3
Rosa rubiginosa		2	2	1	●	●
Anthoxanthum odoratum		6	5	8	2	4
Dactylis glomerata		13	3	4	+	1
Holcus lanatus		2	3	●	+	5
Agrostis capillaris		13	+	+	.	.
Trifolium repens		2	2	2	+	.
Galium aparine		2	2	●	+	2
Hypochoeris radicata		●	+	1	.	+
Crepis capillaris		+	1	2	+	●
Cerastium fontanum		+	1	2	●	+
Hieracium pilosella		+	1	2	2	+
Carex spp.		+	1	.	+	+
Oreomyrrhis ramosa		+	1	+	+	+
Hieracium lepidulum		+	+	1	+	+
Hieracium caespitosum		.	+	1	.	+
Linum catharticum		+	.	●	+	.
Epilobium spp.		+	+	●	.	+
Acaena anserinifolia		.	+	+	+	2

further species with ≤ 40% frequency in all communities

4.4.4.4 *Discaria toumatou* grass-shrubland

4.4.4.5 *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland

a Type with *Polystichum vestitum*

b Type with *Poa cita*

c Type with *Podocarpus hallii*

4.4.4.6 *Coprosma propinqua* – [*Sophora microphylla*] scrub

Table 4.9: Altitude, slope, and aspect (± SE) associated with 'grey scrub' communities.

Community 4.4.	**4.4**	**4.5a**	**4.5b**	**4.5c**	**4.6**
No. of plots	6	5	4	5	4
Altitude (m a.s.l.)	552 ± 58.3	559 ± 51.4	749 ± 106.9	840 ± 18.7	300 ± 50.5
min	200	300	300	700	200
max	1100	1100	1100	1000	400
Slope (°)	25 ± 4.9	14 ± 4.0	44 ± 9.3	31 ± 2.2	14 ± 8.4
min	0	0	20	20	0
max	60	50	90	50	50
Aspect (°)	296 ± 28.4	331 ± 48.7	168 ± 17.8	168 ± 24.9	19 ± 34.6
from	all	all	E	E	NW
to	aspects	aspects	SW	NW	SE

4.4.4.4 *Discaria toumatou* grass-shrubland (14 plots)

The *Discaria toumatou* grass-shrubland comprised 14 plots sampled in habitats of *Carmichaelia australis* and *C. kirkii* along the east of the South Island (Table 4.8). Corresponding with the large geographical range, altitudes varied widely (200 - 1100 m), and plots were located in flat terrain as well as on steep slopes (up to 60°) with varying aspects (Table 4.9).

The community was found in highly modified or disturbed environments, such as roadsides or grazing land. As *Discaria toumatou* benefits from farm management, in particular, the application of phosphate fertiliser, it can form characteristic secondary scrub and shrubland communities in areas of modified pasture (Hunter and Blaschke 1986; Newsome 1987; Wardle 1991). The dominant *Discaria* is usually associated with other small-leaved shrubs, while the ground vegetation consists of species invading from the adjacent grassland (Hunter and Blaschke 1986; Newsome 1987).

In the stands described here, *Discaria toumatou*, together with *Coprosma propinqua, Rosa rubiginosa,* and *Muehlenbeckia complexa*, formed a relatively dense shrub layer with a mean top height of 2.3 ± 0.5 m (Fig. 4.16). An upper shrub tier was not developed, but one plot was sampled in a pine plantation with 15% canopy cover of *Pinus radiata*. Where they occurred, *Carmichaelia australis* and *C. kirkii* were prominent. The ground vegetation was relatively dense and dominated by introduced grasses (*Dactylis glomerata, Agrostis capillaris, Anthoxanthum odoratum*). The plant community was relatively species-poor with 24 ± 2.5 species/plot. Regeneration of both *Carmichaelia* species was observed.

Fig. 4.16: *Discaria toumatou* grass-shrubland community in habitat of *C. australis*, Mackenzie Pass, South Canterbury (GR: I38 159 653).

The *Discaria toumatou* grass-shrubland appeared floristically as a relic community of the *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland described in the following section. Most of the species typical for this richer 'grey scrub' community were present in the *Discaria toumatou* grass-shrubland, but only with low abundance and frequency. The stands could be remnants of previously richer shrubland at these sites, or they could represent successional stages developing to such communities.

4.4.4.5 *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland

Coprosma propinqua – [*Aristotelia fruticosa*] shrubland was mainly found in habitats of *Carmichaelia australis* and *C. kirkii*, although some plots also contained *C. crassicaule* and *C. curta*.

Species composition and structure in this community were closest to the typical ‘grey scrub’ described by Wardle (1991). Wardle also mentions *Carmichaelia* species, in particular, *C. kirkii* and *C. petriei*, as typical components of these communities. *C. petriei* was found associated with *C. kirkii* in several plots of the *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland. The community was relatively species-rich with 31 ± 1.3 species/plot. *Coprosma propinqua* was the dominant shrub, associated with *Aristotelia fruticosa* and other divaricate species, as well as with a number of climbers, in particular, *Muehlenbeckia complexa* and

Clematis marata. The species formed more or less dense stands of scrub or shrubland with a mean top height of 2.7 ± 0.2 m. Apart from the constant presence of *Blechnum penna-marina*, the species composition in the ground layer varied considerably, dependent on the degree of modification, allowing the distinction of three types within the community.

4.4.4.5 a Type with *Polystichum vestitum* (15 plots)

Coprosma propinqua – [*Aristotelia fruticosa*] shrubland in a type with *Polystichum vestitum* was found in habitats of *Carmichaelia kirkii*, sometimes associated with *C. australis*. The plots were spread along the east of the South Island from Marlborough to Central Otago with altitudes ranging from 300 - 1100 m. They were mainly sampled in stream-side habitats, except for one plot which was located in a remnant of lowland podocarp forest in the Canterbury Plains (View Hill). The type with *Polystichum vestitum* occurred on flat terrain as well as on steep slopes (up to 50°) covering all aspects.

Fig. 4.17: *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Polystichum vestitum* in habitat of *C. kirkii*, Scrubby Creek, Benmore Range, South Canterbury (GR: H39 841 437).

The shrub cover was very dense, with *Coprosma propinqua, Aristotelia fruticosa* and *Discaria toumatou* as the prominent shrubs and abundant growth of *Muehlenbeckia complexa* (Fig. 4.17). *C. kirkii* was also prominent with a mean cover of 11%. An upper tier was not developed, except at View Hill, where a canopy of *Dacrycarpus dacrydioides*, *Elaeocarpus hookerianus*, and *Prumnopitys taxifolius* was present with 38% cover.
The ground tier was relatively open in all stands and dominated by adventive grasses (*Anthoxanthum odoratum, Festuca rubra, Dactylis glomerata, Holcus lanatus*). The ferns *Blechnum penna-marina* and *Polystichum vestitum* were prolific, the latter indicating fertile and moist conditions. Mosses and lichens were sparse, but a litter layer was developed covering 26% of the soil surface. Juveniles of the *Carmichaelia* species were usually present.

The abundance of adventive grasses and prominence of *Discaria toumatou* connected this community type floristically with the *Discaria toumatou* grass-shrubland, indicating relatively strong modification of the sites and their surroundings. Most of the stands were located on farmland used for livestock grazing at the time of sampling.

4.4.4.5 b Type with *Poa cita* (7 plots)
The *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Poa cita* comprised seven plots sampled for *Carmichaelia australis* and *C. kirkii* along the east of the South Island. Altitudes varied between 300 and 1100 m. The plots were sampled in a range of different habitats including stream sides and grassy slopes. One plot was located on a steep bank above a now permanently dry creek bed (Murphy's Creek, Otago). The sites were distinctly rockier than those of the previous type. Slopes varied from 20 to over 80°, with E to SW aspects.

The community was characterised by an open shrub tier dominated by *Coprosma propinqua*. Where they occurred, *Carmichaelia australis* and *C. kirkii* were prominent. Similar to the type with *Polystichum vestitum*, the ground layer was dominated by grasses, the adventives *Anthoxanthum odoratum* and *Dactylis glomerata* being the most abundant. However, in this community type, they were associated with a range of species typical of indigenous tussock grassland, indicating a lesser degree of modification of the surrounding vegetation. Mosses and lichens were relatively abundant and a litter layer was developed. Juveniles of the *Carmichaelia* species were usually present.

4.4.4.5 c Type with *Podocarpus hallii* (9 plots)

The *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* was found in habitats of *C. crassicaule, C. curta*, and *C. kirkii*. The plots were sampled in shrubland patches on boulderfields at three locations in southern Canterbury with altitudes between 700 and 1000 m. Slopes ranged from 20 - 50°, with E to NW aspects (Fig. 4.18).

Fig. 4.18: *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* on a boulderfield at Coal Creek, Benmore Range, southern Canterbury.

The shrub cover in this community type was relatively dense with *Podocarpus hallii* as the most prominent species after *Coprosma propinqua* (Fig. 4.19). The other species typical for 'grey scrub' communities also reached relatively high cover values (*Aristotelia fruticosa, Melicytus alpinus, Muehlenbeckia complexa*). The ground layer was very sparse and mainly formed by *Muehlenbeckia complexa* scrambling over boulders and young growth of the shrubs. The tussock grassland species characteristic of the previous type were present, supplemented by *Aciphylla aurea, Viola cunninghamii*, and *Unicinia fuscovaginata*. In contrast, the adventive grassland plants, abundant in all previous ‘grey scrub’ communities, were far less frequent and abundant. Mosses and lichens were nearly absent, but a litter layer was well developed. Regeneration of *Carmichaelia kirkii* was present, while *C. crassicaule* and *C. curta* were only observed as adult plants.

Fig. 4.19: *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* in habitat of *C. kirkii*, Coal Creek, Benmore Range, southern Canterbury (GR: H39 840 321).

The species composition indicated a low degree of modification in this community type. The sites were located in high altitude grazing country with little improved pasture. Furthermore, the nature of the boulderfield habitat was likely to provide relative protection for the plant community by inhibiting the invasion of adventives as well as by providing protection from fire (Wardle 1991). The *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* was restricted to the boulderfield habitat at all sites visited, but the stands might represent remnants of a formerly more widespread vegetation type.

4.4.4.6 *Coprosma propinqua* – [*Sophora microphylla*] scrub (5 plots)

This community was found in habitats of *C. australis* and *C. kirkii*. Two plots were sampled at a site where *C. stevensonii* used to occur, but the population is now extinct (Avon Valley, Marlborough). All plots were located in stream-side habitats of lowland areas (200 - 400 m), on level terraces as well as slopes with gradients up to 50° in varying aspects.

The sampled stands represented later successional stages in the development of ‘grey scrub’ to forest. This succession is typical for ‘grey scrub’ communities in moist lowland valleys (Wardle 1991). Characteristic was the combination of ‘grey scrub’ species with small trees and forest species, *Sophora microphylla*, *Griselinia littoralis*, and *Coprosma crassifolia* being the most common. As the plots were sampled over a wide area in the east of the South

Island ranging from Marlborough to Otago, the species composition of the upper shrub layer varied considerably. For example, at the Avon Valley site, *Kunzea ericoides* was the dominant canopy species (Fig. 4.20), while *Aristotelia serrata* and *Fuchsia excortica* were prominent in *C. kirkii* habitat in Otago (Waihemo). However, despite these differences, the stands were grouped together and characterised as 'grey scrub' community by the prominence of *Coprosma propinqua*, associated with other divaricate shrubs, and the presence of the climbers *Scandia geniculata* and *Muehlenbeckia australis*. The community was relatively species rich, with 30 ± 2.8 species per plot.

Fig. 4.20: *Coprosma propinqua* – [*Sophora microphylla*] scrub at a former site of *C. stevensonii*, Avon Valley, Marlborough (GR: O29 579 384).

The upper and lower shrub tier formed a dense cover of woody plants with a mean top height of over 6 m, creating relatively shady conditions on the ground. The ground layer was open and dominated by adventive grasses (*Holcus lanatus*, *Anthoxanthum odoratum*). *Digitalis purpurea* was also prominent. Mosses were prolific in this community, reflecting the moist conditions, and a relatively dense litter layer was developed. Juveniles of *C. kirkii* were found in one of the plots (Waihemo).

4.4.5 Coastal Grass- and Shrubland

The plots grouped together as coastal grass- and shrubland vegetation were sampled in habitats of *C. australis* and *C. muritai* at coastal sites and in river gorges in the area of southern Marlborough and Canterbury. One shrubland community and two grassland communities were distinguished (Table 4.10). However, the grassland communities seemed to merely represent degraded states of the shrubland community, with degradation being the result of farm management as well as of natural processes, such as drought and the natural instability of the steep habitats (Table 4.11). Juveniles of the *Carmichaelia* species were not found in any of the plots.

4.4.5.1 *Olearia paniculata* shrubland (5 plots)

The *Olearia paniculata* shrubland was found in small stands on a cliff of sandstone conglomerate at Seaview (southern Marlborough), as well as on a steep river bank in the Rakaia River gorge (Canterbury). While the Seaview site is immediately coastal, the cliff rising to approximately 50 m (Fig. 4.21), the Rakaia gorge is located about 60 km inland at 300 m a.s.l.. Both sites were steep, with gradients between 20 and 70° and NW to E aspects.

Fig. 4.21: *Olearia paniculata* shrubland at Seaview, southern Marlborough. The stands are located on a steep cliff of sandstone conglomerate

Olearia paniculata and, where it occurred, *C. muritai* formed a relatively dense shrub layer creating shady conditions underneath (Fig. 4.22). The stands reached a mean top height of 4.6 ± 1.3 m. The ground layer was open and dominated by grasses, with *Dactylis glomerata* being the most prominent. A sparse litter layer was developed and sites were rocky, providing habitat for the rupestral fern *Pyrrosia eleagnifolia*. The community was very species-poor with only 13 ± 2.6 species/plot.

A B

Fig. 4.22: *Olearia paniculata* shrubland in habitat of *C. muritai* at Seaview, southern Marlborough (GR: P28 064 508). The shrubs form a relatively dense upper layer (A), creating shady conditions underneath (B).

The community seemed impoverished compared to coastal scrub communities described by Williams (1982) for other areas of the southern Marlborough coast. According to Williams, *Olearia paniculata* and *Dactylis glomerata* are always prominent, but usually associated with a number of other trees and shrubs, such as *Pseudopanax arboreus, Melicytus ramiflorus, Macropiper excelsum, Corynocarpus laevigatus,* and *Alectryon excelsus*. The poor appearance of the stands described here could be related to the steepness of the habitats. Williams does not state slopes in his descriptions, but a richer community with *Melicytus ramiflorus, M. alpinus, Myoporum laetum*, *Leptospermum scoparium, Kunzea ericoides, Hebe arborea*, and *Cassinia leptophylla* was observed on gentler slopes in the vicinity of the *C. muritai* populations.

Table 4.10: Coastal grass- and shrubland vegetation with *C. australis* and *C. muritai*. All species occurring with a frequency > 40% in at least one community are shown. % cover gives the total cover of the species over all tiers averaged over all plots in the community, ● - < 1% cover, + - frequency ≤ 40% in this community, cover values in brackets refer to planted species.

Community **4.4.**	**5.1**	**5.2**	**5.3**
No. of plots	5	6	3
No. of vascular plant species	13	16	19
Standard error	2.6	2.8	3.2
Top height	4.6	2.0	2.5
Standard error	1.3	0.1	1.5
Mean cover (%)			
Upper shrub tier	63	38	38
Lower shrub tier	.	.	.
Ground tier	36	63	38
Moss and lichen	3	2	1
Litter	16	17	9
Bare ground	17	12	24
Rocks (> 20 cm)	20	5	33
Species (% cover)			
Carmichaelia australis	●	16	5
Juveniles	.	.	.
Carmichaelia muritai	12	(+)	+
Juveniles	.	.	.
Olearia paniculata	30	+	1
Linum monogynum	2	.	+
Bromus hordeaceus	1	+	.
Pyrrosia eleagnifolia	2	.	.
Bromus willdenowii	+	12	.
Poa cita	.	7	.
Sonchus oleraceus	+	●	1
Cirsium vulgare	.	●	.
Rytidosperma racemosum	+	+	27
Echium vulgare	.	.	2
Haloragus erectus	.	.	1
Rosa rubiginosa	.	.	●
Crepis capillaris	.	.	●
Melicytus alpinus	5	4	+
Cytisus scoparius	+	.	6
Dactylis glomerata	5	17	2
Lolium perenne	2	5	2
Muehlenbeckia complexa	+	7	.
Einadia triandra	1	1	.
Asplenium flabellifolium	2	+	.
Dichelachne crinita	.	+	2
Bromus diandrus	.	+	2

further species with ≤ 40% frequency in all communities

4.4.5.1 *Olearia paniculata* shrubland

4.4.5.2 (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland

4.4.5.3 *Rytidosperma racemosum* grassland

Table 4.11: Altitude, slope, and aspect (± SE) associated with plant communities in coastal grass- and shrubland vegetation.

Community **4.4.**	**5.1**	**5.2**	**5.3**
No. of plots	5	6	3
Altitude (m a.s.l.)	50 ± 0	57 ± 19.3	260 ± 102.0
min	.	20	100
max	.	150	380
Slope (°)	40 ± 7.1	33 ± 8.4	50.3 ± 12.5
min	20	0	36
max	70	55	70
Aspect (°)	98 ± 19.7	93 ± 29.6	323 ± 25.9
from	NW	SW	SW
to	E	E	NW

4.4.5.2 (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland (6 plots)

The (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland was recorded in several coastal populations of *C. australis* in Canterbury and at the Seaview cliff site (Fig. 4.23). *C. muritai* did not occur in this plant community, except for some planted individuals. Maximum altitude was 100 m a.s.l., and slopes varied in steepness (max. 60°) and aspect.

The vegetation consisted of very open stands of 2 m tall *C. australis* in a dense matrix of grasses, in particular, *Dactylis glomerata* and *Bromus willdenowii*. A sparse litter layer was present, leaving only 17% of bare ground and rocks. With 16 ± 2.8 species, the community was slightly more diverse than the previous shrubland community.

Fig. 4.23: (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland at Seaview, southern Marlborough. The emerging individuals of *C. muritai* have been planted (GR: P28 064 508).

The (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland was floristically connected to the *Olearia paniculata* shrubland through the presence of *Olearia paniculata* in some of the plots. Furthermore, at the Seaview site, the community occurred on slopes between pockets of *Olearia* shrubland. The prominence of the pasture grasses, *Sonchus oleraceus*, and *Cirsium vulgare* suggested strong modification of this community related to farm management at the sites or in adjacent areas.

4.4.5.3 *Rytidosperma racemosum* grassland (3 plots)

The *Rytidosperma racemosum* grassland was only represented by three plots sampled in populations of *C. australis* on the banks of the Charwell and Conway Rivers, as well as for *C. muritai* in the White Bluffs population. The plots were located at altitudes between 100 and 400 m in SW to NW aspects on generally steeper slopes than the previous community.

The vegetation in the three recorded stands was very open with a sparse shrub cover and a similarly sparse ground layer. The dominant shrubs were adventives, *Cytisus scoparius* in the two plots sampled for *C. australis*, and *Lycium ferocissimum* at the *C. muritai* site (Fig. 4.24). The presence of *Olearia paniculata* again suggested a connection of this community with the *Olearia paniculata* shrubland. At the White Bluffs site, several large *Olearia paniculata* were present, but had died in the year preceding sampling, probably due to drought (J. Clayton-Greene, DoC Renwick, pers. comm.).

Similar to the previous community, the ground vegetation was dominated by grasses, but here *Rytidosperma racemosum* was dominant, while pasture species were greatly reduced or absent. This indicated distinctly drier conditions, reflected also by the presence of *Echium vulgare* and *Crepis capillaris*. Litter was sparse, leaving over 50% of ground and rocks bare. The *Rytidosperma racemosum* grassland had the highest species-richness of the three coastal communities, with 19 ± 3.2 species/plot.

Fig. 4.24: *Rytidosperma racemosum* grassland with *C. muritai* on a cliff face at White Bluffs, southern Marlborough (GR: P28 059 601).

4.4.6 Ruderal and Rupestral Vegetation

Ruderal and rupestral vegetation, other than on Marlborough limestone, was found in habitats of *Carmichaelia australis*, *C. crassicaule*, *C. curta*, and *C. hollowayi*. This vegetation type comprised four distinct plant communities indicating ecological differences between the *Carmichaelia* species (Fig. 4.25, Table 4.12).

The main division was between the fertile habitats associated with limestone outcrops in southern Canterbury and communities of infertile habitats. This distinction was indicated by a group of species typical for more fertile sites (*Poa cita, Poa pratensis, Medicago lupulina*) contrasting *Trifolium arvense* as species characteristic of infertile soils. Further divisions separated grassland of ruderal sites from two rockland communities.

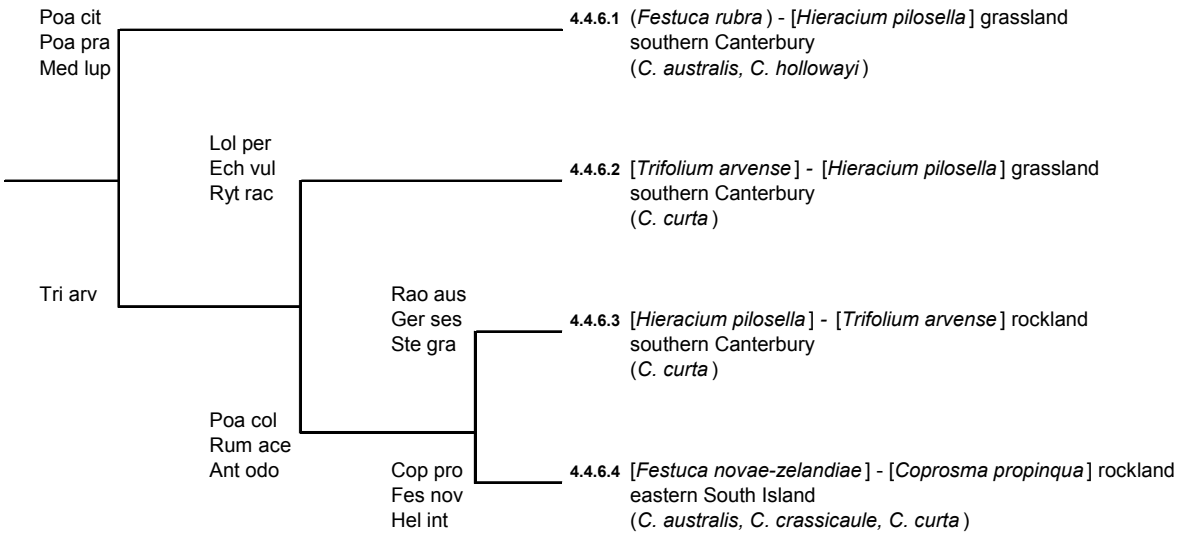


Fig. 4.25: Classification of ruderal and rupestral vegetation into four communities. Not all indicator species are listed; see Table 4.12 for complete list of indicator species and full species names.

4.4.6.1 (*Festuca rubra*) – [*Hieracium pilosella*] grassland (9 plots)

This plant community was found in association with *C. australis* and *C. hollowayi* in the areas of three of the four known populations of *C. hollowayi* (the fourth population was not visited, as it was only discovered in December 2001). The populations are located on limestone outcrops (Otekaieke limestone) emerging on the southern slopes of the Waitaki Valley in South Canterbury at altitudes between 180 and 500 m (Table 4.13). The plant community was recorded from the flat tops of the limestone outcrops as well as from the colluvial slopes below. Accordingly, the gradients of the plots varied between 0 and 30° with aspects ranging from W to N.

Vegetation cover was relatively dense with only 24% of bare ground and rocks (Fig. 4.26). The community showed a combination of species typical for open, rocky sites (e.g., *Echium vulgare, Sedum acre, Arenaria serpyllifolia*) together with plants invading from the adjacent grassland areas. Grasses were the dominant growth form, with the sward forming *Festuca rubra* reaching up to 80% cover in two of the plots (Maori Petroglyphs). Other prominent grass species included *Dactylis glomerata, Festuca novae-zelandiae,* and *Bromus hordeaceus*. *Hieracium pilosella* and *Sedum acre* were the dominant herbs. The plant community showed relatively low species diversity, with 21 ± 2.1 species/plot. Some regeneration of *C. hollowayi* was observed in this community, but it was impossible to distinguish rhizomatous shoots from true seedlings.

Fig. 4.26: (*Festuca rubra*) – [*Hieracium pilosella*] grassland in habitat of *C. hollowayi*, Awahokomo, Waitaki Valley, southern Canterbury (GR: I40 023 085).

4.4.6.2 [*Trifolium arvense*] – [*Hieracium pilosella*] grassland (8 plots)

The [*Trifolium arvense*] – [*Hieracium pilosella*] grassland was only recorded in habitats of *C. curta*. The plots were sampled in populations on road side cuttings along the Waitaki Valley road next to Lake Aviemore and on adjacent farmland (Otematata Station). The altitude for all plots was between 300 and 400 m. Slopes varied from flat terraces to 30° gradients in S, W and N aspects.

The community was characterised by the presence of a group of species typical for dry, open, and infertile sites (*Echium vulgare, Bromus diandrus, B. hordeaceus, Rytidosperma* spp.). The more widespread pasture grass *Lolium perenne* was also constantly present.

Vegetation cover was sparse with the various grass species forming the main component (Fig. 4.27). *Trifolium arvense, Hieracium pilosella,* and *Echium vulgare* were the dominant herbs. The community was species-poor with a mean of 14 ± 0.9 species/plot. Juveniles of *C. curta* were present in some of the plots.

Fig. 4.27: [*Trifolium arvense*] – [*Hieracium pilosella*] grassland in habitat of *C. curta*, roadside cutting along Waitaki Valley road, Lake Aviemore (GR: I40 919 173).

4.4.6.3 [*Hieracium pilosella*] – [*Trifolium arvense*] rockland (10 plots)

Like the previous community the [*Hieracium pilosella*] – [*Trifolium arvense*] rockland was only recorded as habitat for *C. curta*. The plots were sampled over a wider area in the Waitaki River catchment, from sites near Tekapo (Mt John) to Lake Benmore, with altitudes ranging between 300 and 960 m. Plots were located on rocky outcrops with gradients from 0 to 70 ° and SW to N aspects.

The community was characterised by a combination of short tussock grassland species (e.g., *Poa colensoi, Rumex acetosella, Geranium sessiliflorum*) and rupestral and pioneer species typical of dry, infertile sites (e.g., *Verbascum thapsus, Senecio quadridentatus, Cheilanthes*

humilis). Total vegetation cover was very sparse (21%), with *Hieracium pilosella* and *Trifolium arvense* being the dominant species (Fig. 4.28). However, compared to the previous two communities, this community was relatively species-rich with a mean of 25 ± 1.2 species/plot. Juveniles of *C. curta* were usually present.

Fig. 4.28: *Hieracium pilosella-Trifolium arvense* rockland in habitat of *C. curta*, Black Jack's Island, Lake Benmore, southern Canterbury (GR: H39 876 265).

Table 4.12: Ruderal and rupestral vegetation, eastern South Island in habitats of *C. australis*, *C. crassicaule*, *C. curta*, and *C. hollowayi*. All species occurring with a frequency > 40% in at least one community are shown. % cover gives the total cover of the species over all plots in the community, ● - < 1% cover, + - frequency ≤ 40% in this community.

Community	**4.4.**	**6.1**	**6.2**	**6.3**	**6.4**
No. of plots		9	8	10	12
No. of vascular plant species		21	14	25	30
Standard error		2.1	0.9	1.2	1.8
Mean cover (%)					
Vascular plants		74	49	20	38
Moss and lichen		2	1	1	4
Litter		4	5	2	2
Bare ground		19	42	10	2
Rocks (> 20 cm)		5	7	71	63
Species (% cover)					
Carmichaelia australis		+	.	.	+
Juveniles		.	.	.	.
Carmichaelia crassicaule		.	.	.	●
Juveniles		.	.	.	+
Carmichaelia curta		.	2	3	1
Juveniles		.	+	1	●
Carmichaelia hollowayi		11	.	.	.
Juveniles		+	.	.	.
Poa cita		3	.	+	.
Poa pratensis		3	+	.	.
Dichondra repens		4	.	+	+
Medicago lupulina		2	.	.	+
Carduus nutans		●	.	.	.
Trifolium arvense		.	9	4	+
Echium vulgare		2	6	+	+
Lolium perenne		1	6	+	+
Bromus diandrus		+	2	+	+
Rytidosperma maculatum		+	3	.	+
Rytidosperma racemosum		+	3	+	.
Bromus hordeaceus		3	2	.	+
Poa colensoi		2	+	3	5
Rumex acetosella		.	+	3	●
Anthoxanthum odoratum		.	+	2	2
Dichelachne crinita		+	.	2	1
Asplenium flabellifolium		.	.	2	2
Melicytus alpinus		●	+	●	●
Hypochoeris radicata		+	+	●	●
Raoulia australis		.	.	3	+
Geranium sessiliflorum		+	+	2	.
Stellaria gracilenta		.	.	2	+
Cheilanthes humilis		.	.	2	.
Vittadinia australis		+	.	●	+
Dianthus armeria		+	.	●	+
Senecio quadridentatus		.	+	●	+
Verbascum thapsus		.	.	●	+
Coprosma propinqua		+	.	.	7
Rosa rubiginosa		+	+	+	●
Discaria toumatou		+	.	+	●
Festuca novae-zelandiae		4	.	.	9
Anisotome filifolia		.	.	.	3
Wahlenbergia albomarginata		.	.	.	2
Luzula banksiana		.	.	+	1
Celmisia gracilenta		.	.	.	●
Helichrysum intermedium		.	.	+	4
Sedum acre		5	.	.	2
Arenaria serpyllifolia		2	+	+	1
Aira caryophyllea		.	.	.	1
Asplenium richardii		.	.	.	1
Holcus lanatus		.	.	.	2
Crepis capillaris		4	+	+	1
Cerastium fontanum		●	.	+	1
Festuca rubra		15	+	+	+
Dactylis glomerata		6	6	+	3
Hieracium pilosella		7	8	5	3
Elymus solandri		2	2	2	1
Hieracium praealtum		+	+	1	+

further species with ≤ 40% frequency in all communities

4.4.6.1 (*Festuca rubra*) – [*Hieracium pilosella*] grassland

4.4.6.2 [*Trifolium arvense*] – [*Hieracium pilosella*] grassland

4.4.6.3 [*Hieracium pilosella*] – [*Trifolium arvense*] rockland

4.4.6.4 [*Festuca novae-zelandiae*] – [*Coprosma propinqua*] *rockland*

Table 4.13: Altitude, slope, and aspect (± SE) associated with plant communities in ruderal and rupestral vegetation.

Community 4.4.	**6.1**	**6.2**	**6.3**	**6.4**
No. of plots	9	8	10	12
Altitude (m a.s.l.)	396 ± 53.8	319 ± 10.4	662 ± 83.4	518 ± 78.1
min	180	300	300	300
max	500	400	960	1000
Slope (°)	16 ± 4.5	6 ± 2.5	38 ± 6.5	51 ± 4.3
min	0	0	0	30
max	35	30	70	80
Aspect (°)	317 ± 9.2	315 ± 30.7	301 ± 14.1	132 ± 9.2
from	W	S	SW	NE
to	N	N	N	SE

4.4.6.4 [*Festuca novae-zelandiae*] – [*Coprosma propinqua*] rockland (12 plots)

This community was found in habitats of *C. australis*, *C. crassicaule*, and *C. curta* over a wider geographical range than the previous communities. Plots were located in the Tone Valley in southern Marlborough at altitudes of 1000 m, as well as in the Waitaki catchment (300 - 740 m), and at Falls Dam in northern Otago (540 m). The community occupied steep faces on rocky outcrops (30 - 80°) with NE to SE aspects.

Similar to the previous community, the [*Festuca novae-zelandiae*] – [*Coprosma propinqua*] rockland was characterised by a combination of tussock grassland, rupestral and pioneer species, but the actual species assemblage was distinct, as the species typical of dry and infertile sites were less prominent or absent. Instead, several shrub species were present (*Coprosma propinqua, Rosa rubiginosa, Discaria toumatou*), accompanied by a wider range of tussock grassland (*Festuca novae-zelandiae, Anisotome filifolia, Wahlenbergia albomarginata, Celmisia gracilenta*) and rupestral and pioneer species (*Helichrysum intermedium*, *Sedum acre, Crepis capillaris, Arenaria serpyllifolia, Cerastium fontanum, Asplenium richardii, Aira caryophyllea*).

The total vegetation cover was denser, with *Coprosma propinqua* and *Festuca novae-zelandiae* as the dominant species (Fig. 4.29). The sites provided a mosaic of shady and mesic as well as open and dry microsites, reflected in the large variety of species present. The prevalence of more conspicuous tussock grassland plants could be related to the steep slopes protecting the plants from mammalian herbivores. With a mean of 30 ± 1.8 species/plot, this community was the most diverse of the four communities identified under ruderal and rupestral vegetation. *C. crassicaule* and *C. curta* usually showed some regeneration, while *C. australis* was only observed as adult plants.

Fig. 4.29: [*Festuca novae-zelandiae*] – [*Coprosma propinqua*] rockland in habitat of *C. crassicaule* and *C. curta*, Deep Stream, Waitaki Valley, southern Canterbury (GR: I40 001 149).

4.4.7 Rupestral Vegetation on Limestone, Southern Marlborough

4.4.7.1 [*Pachystegia insignis*] – [*Elymus solandri*] rockland

This vegetation type comprised 11 plots sampled in habitats of *Carmichaelia astonii* and *C. australis* (Table 4.14). The data were collected at two localities in southern Marlborough, at which Amuri limestone emerges to the surface. One of these localities was the area of Isolated Stream in the upper Waima (Ure) River Valley, the other a limestone outcrop near the township of Ward. Both areas are located at an altitude of around 200 m (Table 4.15). The vegetation occupied steep rock faces, the plants mainly rooting in cracks of the rock. Vegetation cover was sparse with over 80% of the surface being solid rock or finer rock material. Cryptogams were absent, and a litter layer was not developed.

Pachystegia insignis, a rupestral shrub endemic to the Marlborough region, and the grass *Elymus solandri* were prominent in all plots, characterising this vegetation type as [*Pachystegia insignis*] – [*Elymus solandri*] rockland. A group of mainly adventive herbs and grasses, such as *Dactylis glomerata* and *Medicago lupulina,* was always present, reflecting the relatively fertile habitat conditions. Further associated species allowed the distinction of two types within this community, correlated with the two visited locations. As typical for rupestral plant communities, the precise species composition was largely determined by the seed source available from the surrounding vegetation (Wardle 1991). Regeneration of *C. astonii* was observed at both sites.

4.4.7.1 a Type with *Poa cita* (5 plots)

This community type was associated with *C. astonii* at the limestone outcrop at Ward (Fig. 4.30). The rock faces were NW to SW exposed with the rupestral plant community occurring on all slopes. Gradients reached 40-60°.

The community was characterised by a group of grassland species, such as *Poa cita, Lolium perenne,* and *Poa* colensoi, spreading from the surrounding pasture. The limestone at Ward is relatively crumbly, with finer material on ledges and in cracks possibly facilitating the establishment of grassland plants.

Carmichaelia astonii and *Pachystegia insignis* were the prominent species. Grasses and grassland herbs occurred consistently, but mostly with low abundance. With 16 ± 1.2 species/plot, the plant community was relatively species-poor.

Fig. 4.30: [*Pachystegia insignis*] – [*Elymus solandri*] rockland, type with *Poa cita* in habitat of *C. astonii*, Ward, southern Marlborough.

4.4.7.1 b Type with *Coprosma propinqua* (6 plots)

This type of [*Pachystegia insignis*] – [*Elymus solandri*] rockland was found in the area of Isolated Stream in habitats of *C. astonii* and *C. australis*, the two *Carmichaelia* species often occurring together (Fig. 4.31). The slopes were generally steeper than at Ward (60-90°) with SW to NE aspects.

The community was characterised by the presence of *Coprosma propinqua* and species such as *Brachyglottis monroi, Gingidia montana,* and *Celmisia monroi*, that were also common in the (*Hebe traversii*) shrubland described in section 4.4.4.1. Other species included the rupestral shrubs *Heliohebe hulkeana* and *Helichrysum intermedium*, as well as a number of herbs and grasses characteristic of dry and open habitats (e.g., *Echium vulgare, Vittadinia australis*). With a mean of 26 ± 1.7 species/plot this plant community was considerably more diverse than the community at Ward.

Table 4.14: Rupestral vegetation on limestone in southern Marlborough in habitats of *C. astonii* and *C. australis*. All species occurring with a frequency > 40% in at least one community type are shown. % cover gives the total cover of the species over all plots in the community type, ● - < 1% cover, + - frequency ≤ 40% in this type.

Community **4.4.**	**7**	
Type	a	b
No. of plots	5	6
No. of vascular plant species	16	26
Standard dev.	2.5	3.9
Standard error	1.2	1.7
Mean cover (%)		
Vascular plants	19	18
Moss and lichen	0	0
Litter	1	1
Bare ground	6	0
Rocks (> 20 cm)	75	82
Species (% cover)		
Carmichaelia astonii	12	2
Juveniles	+	+
Carmichaelia australis	.	1
Juveniles	.	.
Poa cita	4	.
Lolium perenne	3	.
Poa colensoi	2	.
Rytidosperma racemosum	2	+
Oreomyrrhis colensoi	3	.
Wahlenbergia albomarginata	2	.
Trifolium dubium	●	.
Convolvulus verecundus	2	.
Coprosma propinqua	.	3
Heliohebe hulkeana	+	3
Brachyglottis monroi	.	●
Helichrysum intermedium	.	●
Trisetum arduanum	.	3
Poa breviglumis	.	2
Rytidosperma buchananii	.	2
Galium perpusillum	.	2
Gingidia montana	.	●
Celmisia monroi	+	●
Gentiana astonii	.	●
Echium vulgare	+	●
Vittadinia australis	.	●
Oxalis exilis	.	●
Epilobium billardiereanum	.	●
Pachystegia insignis	5	7
Elymus solandri	5	3
Dactylis glomerata	2	3
Medicago lupulina	1	2
Crepis capillaris	●	2
Hypochoeris radicata	●	●
Linum monogynum	+	●
further species with ≤ 40% frequency in all communities		

[*Pachystegia insignis*] – [*Elymus solandri*] rockland

4.4.7 a Type with *Poa cita*

4.4.7 b Type with *Coprosma propinqua*

Table 4.15: Altitude, slope, and aspect (± SE) associated with rupestral communities on limestone in Marlborough.

Community **4.4.**	**7a**	**7b**
No. of plots	5	6
Altitude (m a.s.l.)	200 ± 0	207 ± 21.7
min	.	200
max	.	250
Slope (°)	45 ± 3.5	70.8 ± 3.6
min	40	60
max	60	80
Aspect (°)	279 ± 3.7	7.1 ± 23.7
from	SW	SW
to	W	NE

Fig. 4.31: [*Pachystegia insignis*] – [*Elymus solandri*] rockland, type with *Coprosma propinqua* in habitat of *C. astonii* and *C. australis*, Isolated Stream, Waima (Ure) River Valley, southern Marlborough.

4.5 Discussion

The analysis of the plant communities associated with *Carmichaelia* species illustrated a large ecological variability within the genus, with the various species occuring over a wide range of plant communities and vegetation types. This variability is consistent with the large variation in growth habits and other morphological characteristics within the genus (Heenan 1997a, b, 1998a), as well as with pronounced differences in the geographical and climatic ranges of the species (see section 3.3 and Appendix 3

However, the results also showed similarities between the various species, allowing the distinction of five ecological groups. *C. astonii* and *C. hollowayi* were both characterised as rupestral species, while *C. crassicaule* and *C. vexillata* emerged as typical grassland species. *C. kirkii*, *C. muritai*, and *C. stevensonii* formed a group of scrub and shrubland species, and *C. curta* and *C. juncea* were connected by their status as typical pioneer species. *C. australis* was distinct from the other species by its wider ecological range, characterising this species as ubiquitous. The division of the *Carmichaelia* species into ecological groups is discussed in more detail below. In addition, inferences on potential threats to the *Carmichaelia* species are drawn, based on the characteristics of their current habitats and plant communities.

A feature common to most of the communities described in this study was the prominence of introduced species, indicating a strong degree of modification of the *Carmichaelia* habitats. Modification and invasion by introduced plants are factors affecting almost all habitat types in New Zealand today (Wardle 1991). This poses a particular challenge to the conservation of rare species, as their management has to deal with these modified communities in trying to maintain suitable habitat for natives, while the causes and consequences of invasions and the dynamics of the modified plant communities are still poorly understood (e.g., Walker and Lee 2000; Duncan et al. 2001; Walker and Lee 2002).

4.5.1 Rupestral Species: *C. astonii* and *C. hollowayi*

The ecological preferences of *C. astonii* and *C. hollowayi* appeared to be similar, as both species were restricted to a single, mainly rupestral plant community characterised by base-rich substrate (c.f. Druce and Williams 1989; Wardle 1991; Heenan 1995, 1996b). While *C. astonii* occurs on Amuri limestone in Marlborough, *C. hollowayi* occupies limestone areas

in southern Canterbury, both species being geographically restricted to their respective areas. The present range restriction of these species is likely to be natural, as rock outcrop habitats often provide sufficient isolation to promote plant speciation. In particular, in New Zealand, emergent limestone usually occurs confined to island-like areas (Wardle 1991). More than one third of the species considered to be rare in New Zealand are species of steep and rocky terrain, and local endemism is particularly common amongst basicole species (Molloy 1994; Molloy et al. 1999b; Rogers and Walker 2002). In addition, the southern Marlborough region is known for its high proportion of endemic species; four other *Carmichaelia* species are restricted to this area (Wardle 1991; Heenan 1996a).

The plant communities *C. astonii* and *C. hollowayi* occurred in were strongly influenced by the vegetation types present in the areas adjacent to the rock outcrop habitats. This is characteristic for rupestral plant communities (Wardle 1991). *C. astonii* was found in two types of [*Pachystegia insignis*] – [*Elymus solandri*] rockland, corresponding with the two visited locations, and the community is likely to further vary at other locations. For example, Druce and Williams (1989) describe *C. astonii* from an open shrubland community with *Discaria toumatou, Melicytus alpinus*, and *Pimelea aridula* in the Ben More - Chalk Range area. As all sites of *C. hollowayi* are set in a matrix of modified grassland used for livestock grazing, this species was only found in one community, characterised by the presence of pasture species.

Threats

The invasion of species from surrounding vegetation types into the rupestral habitats could pose a threat to the persistence of the *Carmichaelia* species, in particular, by inhibiting their regeneration (Heenan 1996b; Dopson et al. 1999). This did not appear to be the case for *C. astonii*, as both types of the [*Pachystegia insignis*] – [*Elymus solandri*] rockland were characterised by a sparse vegetation cover. Sites were steep (40 – 80°) and usually without any top soil, limiting the establishment of more closed vegetation. Consistent with this, regeneration of *C. astonii* was observed at both visited locations. Furthermore, both populations seemed healthy, as plants of all size classes were present.

In contrast, the vegetation in habitats of *C. hollowayi* was relatively dense. The community was characterised as (*Festuca rubra*) – [*Hieracium pilosella*] grassland, the name reflecting the dense grass cover with dominance of introduced species. As the habitats of *C. hollowayi* are not as steep (0 – 35°), patches of fine rock material and shallow top soil provide suitable microsites for invasion by species from the surrounding areas. These areas have been strongly modified since the beginning of human settlement, and simultaneously, species

composition and community structure in the habitats of *C. hollowayi* are likely to have changed dramatically (c.f. Molloy et al. 1999b). During this study, regeneration of *C. hollowayi* was observed, although it was impossible to distinguish vegetative spread from true seedlings, as young rhizomatous shoots show juvenile morphology. However, two of the three assessed populations are very small, with two and eight plants respectively, clearly indicating a lack of recruitment.

The exposed habitats of *C. astonii* seemed to also protect the plants from mammalian herbivores, as very little browse damage was observed during the field work for this study, despite the site at Ward being accessible to livestock. However, severe browse damage has been reported for *C. astonii* in the past (S. Courtney, DoC Nelson, pers. comm., records in CHR, AK, WELT). As habitats of *C. hollowayi* are less steep, herbivory by introduced mammals is more likely to pose a threat to this species (Heenan 1996b; and see chapter 6).

The presence of *C. australis* appeared to pose an additional threat to *C. hollowayi*, as the two species hybridise (Heenan 1998a). Such hybrids were observed in at least two of the four populations of *C. hollowayi*, and ongoing genetic introgression could lead to the extinction of the true *C. hollowayi* genotype in these populations. Anthropogenic modification of the adjacent areas is likely to represent the ultimate cause for this threat, as land clearance and farm management practices have disrupted previous speciation barriers by assisting the spread of *C. australis* (see section 4.5.5).

In contrast to this situation, *C. australis* appeared to be a natural component in the [*Pachystegia insignis*] – [*Elymus solandri*] rockland, where it was associated with *C. astonii* (c.f. Druce and Williams 1989; Wardle 1991). Hybrids between these two *Carmichaelia* species have not been observed (Heenan 1998a).

4.5.2 Grassland Species: *C. crassicaule* and *C. vexillata*

C. crassicaule and *C. vexillata* were both characterised as species of grassland vegetation with the majority of their populations occurring in this vegetation type.

C. crassicaule showed a preference for relatively unmodified communities, as most of the populations were found in the (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock-grassland (4.4.3.3) and [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland (4.4.3.4). The latter community corresponded most closely with the heath vegetation described by Wardle (1991) to be typical for this species. A preference of *C. crassicaule* for less degraded communities

was further indicated by the fact that no regeneration was found in the highly degraded [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield (4.4.3.1). However, *C. crassicaule* also appeared relatively versatile with respect to habitat types, as it was found in one of the shrubland communities (4.4.4.5 c) and the [Festuca novae-zelandiae] – [Coprosma propinqua] rockland (4.4.6.4). *C. crassicaule* seemed to have spread into these communities from adjacent grassland areas, together with other typical tussock grassland species.

Compared to *C. crassicaule*, *C. vexillata* expressed little versatility with respect to habitat type, as it was restricted to the communities identified within grassland vegetation. However, within these communities, *C. vexillata* seemed more tolerant to degradation than *C. crassicaule*, as it occurred with higher frequency in the degraded communities (4.4.3.1, 4.4.3.2) and was not found in the least modified [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland (4.4.3.4). However, this difference in tolerance to degradation between the two species could also be an artefact, caused by the fact that both species were often browsed to ground level, and while browsed individuals of *C. vexillata* are still conspicuous, appearing as a dense mats of stems, browsed individuals of the single-stemmed *C. crassicaule* are easily overlooked. Sheep and rabbit proof fencing of a highly degraded grassland area in the Mackenzie Basin resulted in the appearance of mature *C. crassicaule* plants, re-sprouting from old root stocks, where the species had previously seemed absent (N. Ledgard, Forest Research, pers. comm.).

Threats

Herbivory by introduced mammals seemed likely to represent a threat to both, *C. crassicaule* and *C. vexillata*, as severe browse was frequently observed (c.f. Dopson et al. 1999; chapter 6). In many populations of *C. crassicaule*, tall plants were only found growing inside dense *Chionochloa* tussocks or on exposed ledges, where sheep and other mammals were unlikely to graze, while plants in more accessible places were small and severely damaged.

A further threat to the persistence of *C. crassicaule* and *C. vexillata* could arise from changes in the composition and structure of their grassland habitats. The majority of grasslands in the eastern South Island of New Zealand are induced communities, brought about by land clearance since the beginning of human settlement (Mc Glone 2001). Their species composition and structure, therefore, depend largely on the imposed management. Further degradation is likely to lead to a decline of the *Carmichaelia* species. This was indicated by the preference of *C. crassicaule* for less degraded communities, and also by the fact that, although *C. vexillata* appeared more tolerant to degradation, it was not found at sites comparable to the most highly degraded grassland community described in this study

(4.4.6.3). Similarly, 'amelioration' of the grassland areas, i.e. irrigation, application of fertiliser, or oversowing with pasture species, would lead to a decline of the species, as no populations of *C. crassicaule* or *C. vexillata* were found in such modified habitats. However, cessation of all management and the onset of natural succession could also pose a threat to the *Carmichaelia* species, e.g. through enhanced invasion of adventives or the development of shrubland vegetation (Meurk et al. 1989; Lord 1990; Calder et al. 1992; Rose et al. 1995; Bellingham 1998; Walker 2000).

4.5.3 Scrub and Shrubland Species: *C. kirkii*, *C. muritai*, *C. stevensonii*

C. kirkii, *C. muritai*, and *C. stevensonii* were characterised as species of scrub and shrubland, however, at the same time, each of these species was distinct with respect to the communities in which they occurred.

C. kirkii showed the widest ecological range growing in most of the scrub and shrubland communities described in this study. It also expressed high versatility regarding the seral stage of vegetation, as it was present in earlier successional (4.4.4.1) as well as later successional communities (4.4.4.3, 4.4.4.6). The [*Leptospermum scoparium*] / (*Coriaria arborea*) shrubland (4.4.4.2) was not found as habitat of *C. kirkii*, probably because it represented a lowland community of southern Marlborough, while *C. kirkii* is restricted to higher altitudes in this region (see Appendix 3). Most of the presently known populations of *C. kirkii* were found in 'grey scrub' vegetation, in particular, the *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland (4.4.4.5), with highest prominence in the most modified type (Type with *Polystichum vestitum*, 4.4.4.5 a). However, the low number of plots recorded in the less modified communities, in particular the [*Podocarpus hallii*] shrubland (4.4.4.3) and the *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* (4.4.4.5 c), could be due to the fact that these habitats are rare, rather than that they represent marginal habitat for *C. kirkii*. *Podocarpus hallii* forest and scrub used to be a widespread vegetation type throughout the eastern South Island until deforestation by human settlers (Mc Glone and Basher 1995; Mc Glone and Moar 1998; Mc Glone 2001). The extant stands recorded here, were mostly located at sites that provided at least partial protection from fire, such as gullies or boulderfields, and therefore, seemed likely to represent remnants of formerly more widespread communities.

The restricted geographical ranges of the southern Marlborough endemics *C. stevensonii* and *C. muritai* coincided with their narrow ecological ranges, as these species were only found in one and two communities respectively. Both species are confined to very steep and

unstable habitats, but, while *C. muritai* appears as a strictly coastal species growing on exposed cliffs of sandstone conglomerate, *C. stevensonii* occurs at relatively high altitudes in the Inland and Seaward Kaikoura Ranges.

The habitat of *C. muritai* was characterised by a poor type of coastal shrubland and a grassland community probably derived from degradation of this shrubland. Whether this species used to be more widespread, possibly as part of richer *Olearia paniculata* shrubland communities, or whether the steep and unstable cliff areas it is found in today form its optimal habitat, remains speculation.

C. stevensonii is likely to have been more widespread in the past, as the stands of [*Podocarpus hallii*] shrubland (4.4.4.3) it occurred in are probably remnants of a formerly more widespread vegetation type (as above for *C. kirkii*). Furthermore, *C. stevensonii* used to occur in several lowland locations, from which it has now disappeared. These lowland sites are characterised by the presence of the later successional *Coprosma propinqua* – [*Sophora microphylla*] scrub (4.4.4.6).

Threats

The main threat for all three species appeared to be habitat destruction. This was particularly apparent for *C. kirkii*, as land clearance and intensive land use have only recently led to the extinction of some of its populations (e.g., at Gimmerburn, Central Otago, last recorded in 1996) or reduced populations size to only a few individuals leaving little prospect of long term persistence (e.g., populations at Banks Peninsula). The habitats of *C. muritai* and *C. stevensonii*, in contrast, seemed more threatened by natural, catastrophic events, as they are located on very steep and unstable slopes.

Competition with introduced plants appeared to present a threat, in particular to *C. muritai*. The two known populations of this species are located 9.5 km apart at the southern Marlborough coast (Seaview and White Bluffs), and the recorded plant communities allowed a comparison of these two localities illustrating the significance of competition as a threat to the species.

At White Bluffs, *C. muritai* occurred along the cliff face on narrow, eroded ridges and in steep gullies, as well as on the colluvial slopes between these features. The colluvial slopes were characterised by the presence of the relatively open *Rytidosperma racemosum* grassland (4.4.5.3). Although no regeneration was found in the actual sample plot, the population appeared to be in a healthy state, as plants of all size classes were present. The smallest

plant (c. 20 cm tall) was found on one of the colluvial slopes, indicating that these areas provided suitable conditions for regeneration of *C. muritai*.

At Seaview, in contrast, *C. muritai* occurred only on steep ridges and in gullies, in small stands of *Olearia paniculata* shrubland (4.4.5.1), but was absent from colluvial slopes. At this site, these slopes were occupied by the (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland (4.4.5.2), which was characterised by a very dense layer of ground vegetation. Most plants in the Seaview population were of similar size, and presumably age, indicating a general lack of recruitment in the population. The few young plants that were present grew immediately next to some of the adults in the *Olearia paniculata* shrubland (c.f. Williams et al. 1996).

The distribution of *C. muritai* at the two sites, and in particular, the distribution of regeneration, suggested that the dense ground layer in the (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland represented a threat to the persistence of the species by inhibiting successful regeneration. In addition, the fact that the dense shrub layer in the *Olearia paniculata* shrubland did not prevent regeneration indicated that *C. muritai* is more vulnerable to immediate root competition during establishment than to competition for light. These observations were consistent with the findings in the competition experiments (chapter 5).

The impact of introduced mammalian herbivores poses an additional threat to the persistence of the three scrub and shrubland species. In particular, the numerous introduced ungulates, domestic and feral, are known to open up dense stands of shrubland, facilitating invasion by weeds, and exposing the young growth of trees and shrubs to direct predation (Fox and Fox 1986, Jesson et al. 2000). Numerous studies in New Zealand have documented drastic changes in structure and composition of indigenous scrub and forest communities resulting from herbivore pressure (e.g., James and Wallis 1969; Veblen and Stewart 1980; Allen et al. 1984; Campbell 1990; Nugent et al. 2001).

Most extant populations of *C. kirkii* are subject to herbivore pressure by livestock, as they are located on agricultural land used for grazing. The habitats of *C. muritai* and *C. stevensonii*, in contrast, are mainly subject to the impact of feral mammals. The *C. muritai* population at Seaview is fenced against larger mammals, and rabbits are unlikely to pose a problem, as the grass cover on the colluvial slopes is very dense, but possum browse was observed on the adult plants. The more open vegetation cover at the White Cliffs population of *C. muritai* is likely to provide better habitat for rabbits, and small numbers of ungulates are also likely to be present (chamois and goats, J. Clayton-Greene, DoC Renwick, pers. comm.). In 1971,

Wardle predicted drastic changes caused by high ungulate pressure for *Podocarpus hallii* forests and subalpine scrub in the Seaward Kaikoura Ranges, which represent habitats of *C. stevensonii*. Although ungulate numbers in these areas have since been reduced, their presence could still pose a threat to these communities and the persistence of *C. stevensonii*. Severe browse damage on young plants of *C. stevensonii* was observed.

4.5.4 Colonisers: *C. curta*, *C. juncea*

The present and historic habitats of *C. curta* and *C. juncea* identified these two species as colonisers, adapted to open sites with little competition from associated plants. Although the two species differ widely in their geographical as well as climatic ranges (see section 3.3 and Appendix 3), they were both found in communities with very open, low growing vegetation. Their status as colonisers is further supported by their rapid development from juveniles into adults (pers. obs.). *C. curta* and *C. juncea* were the only species that flowered within one year in the glasshouse; the first *C. curta* flowered even after three months, at the end of the root competition trial. In the field, both species appeared relatively versatile with respect to their habitats, growing in grassland communities as well as on rock outcrops. *C. juncea* even seemed tolerant to salt-spray at its cliff face location in Northwest Nelson.

Most of the *C. curta* populations were found in ruderal or rupestral communities characterised by dry and infertile conditions (4.4.6.2, 4.4.6.3), as well as in severely degraded grassland (4.4.3.2). These seemingly unfavourable habitats appeared to provide adequate conditions for the persistence of *C. curta*, as regeneration was usually present. As the species was not found in any of the less degraded grassland communities described in section 4.4.3 , it separated clearly in its ecology from *C. crassicaule* and *C. vexillata*. One plot was recorded in a stand of *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland in its type with *Podocarpus hallii* (4.4.4.5 c), where *C. curta* was associated with *C. kirkii*. *C. curta* appeared to be present as a rupestral element in this boulderfield community, as it was also found on several small rock outcrops in the vicinity.

The prominence of *C. curta* in apparently unfavourable habitats, could be the result of a displacement process, caused by human land use, in particular, the introduction of pasture plants (Given 1994; Foster 1999). On more favourable sites, introduced species are usually aggressive invaders, out-competing natives adapted to sparse vegetation cover. The indigenous species can often only persist at sites which the invaders are unable to colonise (Wardle 1991; Given 1994). This displacement process has been observed for a number of coloniser species around the world (Prince and Hare 1981; Cropper 1993; Foster 1999). In

New Zealand, Wardle (1991) describes it for *Rytidosperma* species, which were found as a major component in the [*Trifolium arvense*] – [*Hieracium pilosella*] grassland (4.4.3.2) associated with *C. curta*. Furthermore, the same displacement process is thought to have led to the serious decline of a number of native shrubs in New Zealand (e.g., de Lange and Silbery 1993; Rogers 1996; Shaw and Burns 1997; Widyatmoko and Norton 1997).

C. juncea also seemed likely to have been affected by this process, documented by the numerous populations known to have become extinct. Although only few accurate descriptions exist, all historic records point towards relatively open pioneer habitats such as lake shores and creek margins to be typical for *C. juncea*. The most detailed record describes its habitat at Lake Lyndon in January 1896 (WELT): “2600 ft, just where the tussock merges into mud of lake, edge of tussock adjoining shore of Lake Lyndon, in clayey ground, facing south, but exposed to full sunshine”. Similarly, the present populations of *C. juncea* are located in open pioneer vegetation. Although the [*Raoulia* hookeri] – [*Holcus lanatus*] grassland (4.4.1.2) represented a later successional community, vascular plant cover was still relatively sparse, providing open conditions suitable for regeneration of *C. juncea*. The species was not found in more advanced communities, as also noted by Wardle (1991) and Norton et al. (1998). Competition with introduced plant species, therefore, seems likely to have played a role in the extinction of *C. juncea* from its historical sites, especially, as most of these were located in the more strongly modified eastern areas of the South Island.

Threats

The present habitats of *C. curta* and *C. juncea* seemed to provide adequate conditions for the persistence of the populations, as regeneration was usually observed.
Most sites of *C. curta* appeared sufficiently unfavourable for adventive species to limit their invasion, although, especially in some of the rock outcrop populations, beginning invasion by shrubs and trees (*Rosa rubiginosa, Cytisus scoparius*, and *Pinus* spp.) indicated a future threat. The presently occupied grassland areas are most threatened by the intensification of farm management, as pasture ‘improvement’ by cultivation, fertiliser application, and oversowing would destroy suitable habitat. This land conversion has already led to a significant range restriction of *C. curta* (Grove 2001; Appendix 3). Increased grazing pressure could also lead to a decline of the species, although plants seemed relatively tolerant to browse, probably due to their rhizomatous growth habit (Heenan 1995; Grove 2001).

The present habitats of *C. juncea* also showed relatively limited invasion by adventive species. The main threat to the species appeared to arise from the interaction between the

natural dynamics of the habitat and the impact of mammalian herbivores. As the latter can prevent seed production in existing populations (chapter 6), they limit the availability of seeds for regeneration. In the long-term, this is likely to lead to a failure of recolonisation of *C. juncea* after major disturbance events. A further threat for *C. juncea* results from hybridisation with *C. australis* (Northwest Nelson, S. Courtney, DoC Nelson, pers. comm.) and *C. arborea* (South Westland, pers. obs.).

4.5.5 Ubiquitous Species: *C. australis*

C. australis differed from all the other *Carmichaelia* species in its ecological versatility, as it occurred in a range of vegetation types and plant communities, from grassland over shrubland to rupestral habitats (c.f. Heenan 1996b; Wardle 1991). The early pioneer vegetation of South Westland represented the only vegetation type where *C. australis* was not found, indicating its status as a later successional species. In South Westland, *C. australis* is mainly found in wetland areas (D. Norton, UoC, pers. comm.).

Most of the eastern populations were found in shrubland communities, including the coastal *Olearia paniculata* shrubland (4.4.5.1), characterising *C. australis* as a shrubland plant. Its distribution over the various plant communities further indicated that this species benefits from disturbance and degradation, as in most vegetation types *C. australis* showed prominence in the more degraded or disturbed communities, such as the *Discaria toumatou* grass-shrubland (4.4.4.4), the *Hieracium pilosella* herbfield (4.4.3.2), and the two coastal grassland communities (4.4.5.2, 4.4.5.3) derived through degradation of the *Olearia paniculata* shrubland. Furthermore, *C. australis* was not found in the two least degraded grassland communities (4.4.3.3 d, 4.4.3.4). However, *C. australis* was also not found in the most highly degraded communities within grassland and ruderal and rupestral vegetation (4.4.3.1, 4.4.6.2, 4.4.6.3), suggesting that the species is restricted to more mesic and especially fertile sites (c.f. Heenan 1997b; Appendix 3). Consistent with this, it was present in the two communities on limestone substrate (4.4.6.1, 4.4.7).

The wide geographical as well as ecological spread of *C. australis* and, in particular, its apparent benefit from disturbance and degradation support the current view of *C. australis* as a successful and common species, not in need of conservation management (Heenan 1996b; de Lange et al. 1999).

4.6 Conclusions

The results illustrated that *Carmichaelia* species vary considerably in their ecology, despite their phylogenetic proximity. While some species were characterised as typical colonisers being adapted to very open vegetation (*C. curta*, *C. juncea*), others appeared to be later successional grassland (*C. crassicaule*, *C. vexillata*) or shrubland species (*C. kirkii*, *C. muritai*, *C. stevensonii*). *C. astonii* and *C. hollowayi* were characterised as specialised rupestral species, while *C. australis* emerged as ubiquitous species. This variability between the species highlighted the fact that in the conservation management of *Carmichaelia* species, no single strategy would be suitable for all of them. As habitat requirements and preferences vary, the factors representing threats to the various species are likely to also vary, demanding different management strategies.

However, the results also illustrated that, despite the large variation, species showed ecological similarities, allowing the distinction of five ecological groups. These groups might allow for a more efficient approach to the conservation management of *Carmichaelia* species than could be achieved by case-by-case studies. Further research regarding the characteristics of the ecological groups and, in particular, their differential vulnerability to potential threats could provide the basis for “group-based” management strategies. Such research would, furthermore, provide insight into the general dynamics of threats in relation to the ecological characteristics of species. The second part of this thesis, therefore, takes such an approach by investigating the vulnerability of *Carmichaelia* species to the impacts of introduced plants and introduced mammalian herbivores.

5 The Impact of Competition with Introduced Plants

5.1 Introduction

This chapter investigates the significance of competition as a threat to the persistence of *Carmichaelia* species. It explores, in particular, whether the vulnerability of the species to this impact is correlated to their ecology and other species characteristics, as such correlations would allow predictions regarding the vulnerability of species to competition, and therefore, aid in priority setting for the conservation management of threatened plants.

Competition with introduced plants has been observed as a likely threat to indigenous plant taxa world wide (D'Antonio and Vitousek 1992; Vitousek et al. 1996, 1997; Mack et al. 2000; D'Antonio et al. 2001). Plants of isolated regions, such as the islands of Hawaii, Indonesia, and New Zealand, seem particularly affected (Mace et al. 2001). As natives of these areas have evolved in relative isolation, with very limited immigration over time, they seem unable to cope with the flood of new species that have arrived in the wake of human colonisation.

New Zealand's indigenous flora evolved in relative isolation for 80 million years, but since the arrival of humans, more than 10 000 plant species have been introduced, and more than 2000 of these have established with populations in the wild, almost outweighing the number of native species (Webb et al. 1988; Heenan et al. 1999; Williams and West 2000). A shift in the composition of plant communities towards a larger exotic component has been widely documented (e.g., Treskonova 1991; Wardle 1991; Rose et al. 1995), and competition with introduced plants has been suggested as one likely mechanism causing the decline of many native species in New Zealand (Wardle 1991; Walker 2000).

Generally, introduced plants are believed to be stronger competitors than indigenous species (Wardle 1991). For example, Moen and Meurk (2001) found that introduced *Hieracium* are superior in competition with a number of native New Zealand herbs. Similarly, the many introduced sward grasses are likely to out-compete indigenous bunch grasses (Wardle 1991). Such competitive relationships have been found for introduced sward and native bunch grasses in North America (Gordon et al. 1989; Davis et al. 1998; Carlsen et al. 2000). The main threat introduced plants impose on native species seems to lie in their detrimental effects on regeneration (Williams 1997; Timmins and Reid 2000; Walker 2000). Studies in shrub-grassland systems of North America and Hawaii have shown that invasive plants, in particular grasses, are able to prevent the successful establishment of native shrubs (e.g.,

Eliason and Allen 1997; D'Antonio et al. 1998; Davis et al. 1998). Reduced regeneration of natives in the presence of aggressive invaders has also been observed in New Zealand (e.g., Kelly and Skipworth 1984; Wiser et al. 1997; Ogle et al. 2000), and has repeatedly been suggested as a problem for rare plants (e.g., Williams and Timmins 1990; Morgan and Norton 1992; Rogers 1996; Williams et al. 1996; Shaw and Burns 1997; Widyatmoko and Norton 1997; de Lange et al. 2000; Norton 2001).

Species are known to vary in their vulnerability to competition (Keddy 2001). However, exactly which species are likely to be the better competitors, and which are the more vulnerable to displacement is largely unclear, as the underlying mechanisms determining the competitive ability of species are poorly understood (Keddy 2001). A number of studies have attempted to find patterns in the correlation of competitive ability with other species characteristics to clarify this point, but so far, the results show little consistency (Grime 1979; Gaudet and Keddy 1988; Tilman 1988; Goldberg 1996).

The negative correlation between competitive ability and relative growth rate has probably found the widest consensus amongst experimental competition studies to date, in particular in relation to the shade tolerance of species (Grime and Jeffrey 1965; Augspurger 1984; Williams and Buxton 1989; Ebbett and Ogden 1998). Furthermore, Grime (1979) and Tilman (1988) suggest a correlation between the competitive ability of species and their habitat. This relationship seems generally accepted, as it has been widely used, e.g. in studies on forest dynamics (e.g., Williams and Buxton 1989; Ebbett and Ogden 1998). As plants adapt to the vegetation types in which they grow, their competitive abilities reflect the conditions they face in these habitats (Grime 1979; Tilman 1988; Goldberg 1996).

The conservation management of rare and threatened species needs to consider the potential threat introduced plants pose to indigenous taxa. However, weed control is usually labour intensive, and in most cases, the total removal of adventive species and a return to the original habitat conditions is not possible. Because of this and the limitations imposed by the usually restricted financial resources available, it seems necessary to clarify the significance of competition as a threat. Priorities need to be set on the most vulnerable species, and their conservation requirements need to be determined, to ensure successful and (cost-) effective management.

5.2 Objective and Research Approach

In the attempt to contribute to a better understanding of the impact of competition on threatened species, this study explored whether the vulnerability of species to this impact could be predicted from their habitat ecology. Correlations of competitive ability with other species characteristics were also investigated.

I used eleven species of indigenous New Zealand broom, *Carmichaelia*, as study species. These were the ten species described in section 3.3 , as well as *C. petriei* as an additional common species. Introduced plants have invaded almost all vegetation types in New Zealand (Wardle 1991; Williams and West 2000), and chapter 4 illustrated that they often dominate in the habitats *Carmichaelia* species are found in today. Increased levels of competition, therefore, are believed to pose one of the main threats to the persistence of *Carmichaelia* species in the wild (Purdie 1985; Heenan 1995, 1996b; Williams et al. 1996).

Two experiments were undertaken to distinguish between the effects of above ground competition for light and below ground competition for soil resources. Shoot and root competition represent two independent mechanisms that affect species in different ways, and both need to be considered, if we want to fully understand the impact of introduced plant species on native taxa (Casper and Jackson 1997).

The focus of the study lay on the initial phase of seedling establishment, as this life stage is considered to be the most vulnerable, and at the same time, the decisive life stage for the persistence of species (Peart 1989; Larcher 1995; Goldberg 1996). Although the experiments were limited to the first four months of establishment, the results, therefore, are nonetheless likely to give indications for the long-term persistence of the *Carmichaelia* species under competitive conditions.

5.3 Definitions

Competition can be defined as “the negative effects that one organism has upon another by consuming, or controlling access to, a resource…” (Keddy 2001, p. 5). Whether or not an organism performs well in a competitive situation depends on the competitive ability of this organism. Its competitive ability is determined by two separate components (Goldberg 1990, 1996). One is the ability of the organism to reduce the performance of its neighbours, which is termed ‘competitive effect’. The other component is the ‘competitive response’, a measure for the ability of the organism to persist in the presence of other competitors. Both, competitive effect and response contribute to the overall competitive ability of an organism, but their relative importance varies with the symmetry of the competitive relationship (Goldberg 1990).

In the case considered here, the establishment of seedlings in competition with existing vegetation, the relationship is strongly asymmetrical (Goldberg 1990). While the surrounding vegetation is likely to exert a strong competitive effect on emerging seedlings, the seedlings themselves are unlikely to have any effect on their surroundings. The establishment success of seedlings, therefore, can be assumed to depend entirely on the strength of their competitive response (Goldberg 1990, Keddy et al. 1998).

5.4 Hypotheses

The ecological grouping developed in chapter 4 allowed the establishment of hypotheses predicting the competitive ability of the *Carmichaelia* species based on the levels of shoot and root competition prevalent in their typical habitats (Table 5.1).

The habitats described in chapter 4 do not necessarily reflect the competitive conditions in the original habitats of the *Carmichaelia* species, prior to human settlement. However, as all species have been found to regenerate in their current habitats, they were assumed to be adapted to the current competitive conditions. Typically low levels of shoot or root competition in a habitat type were assumed to be associated with a weak competitive ability, and thus, species of such habitats were expected to show weak competitive responses. Conversely, if the current habitats were characterised by high levels of competition, the species were assumed to have a strong competitive ability, showing strong competitive

responses in the experiments. The competitive conditions in the habitats were estimated using the descriptions provided in chapter 4, as well as other competition studies.

Table 5.1: Ecological groups within *Carmichaelia* (chapter 4), levels of shoot and root competition affecting seedling establishment in typical habitats, and expected competitive response (CR) of the species.

Ecological group (see chapter 4)	**Rock outcrop species**	**Grassland species**	**Scrub and shrubland species**	**Colonisers**	**Ubiquitous species**
Species	*C. astonii*	*C. crassicaule*	*C. kirkii*	*C. curta*	*C. australis*
	C. hollowayi	*C. vexillata*	*C. muritai*	*C. juncea*	*C. petriei*
			C. stevensonii		
Level of					
Shoot competition	Low	Low - Intense	High	Low	Low - High
Root competition	High	High	Low	Low	Low - High
Expected CR					
Shoot competition	Weak	Strong	Strong	Weak	Strong
Root competition	Strong	Strong	Weak	Weak	Strong

Rock outcrop habitats are generally characterised by relatively low levels of shoot competition, as the vegetation is usually open, but high levels of root competition because of the generally limited rooting space (Keogh 2000, after Keddy 2001). *C. astonii* and *C. hollowayi* were, therefore, expected to show weak responses to shoot competition, but strong responses with respect to root competition.

Grassland vegetation is likely to vary in the level of shoot competition depending on vegetation cover and height. While degraded and short tussock grasslands are relatively open, providing low levels of shoot competition, tall tussock grasslands with a dominance of *Chionochloa* species are likely to impose intense competition for light during seedling establishment. As both, *C. crassicaule* and *C. vexillata* were found in tall tussock communities (chapter 4), these species were assumed to be adapted to intense shoot competition and, therefore, to be capable of strong competitive responses. Levels of root competition are likely to be high in all grassland vegetation, due to the prevalence of shallow rooting grasses and forbs, requiring strong competitive responses of seedlings.

Scrub and shrubland habitats were assumed to provide conditions with intense shoot, but little root competition. *C. kirkii*, *C. muritai*, and *C. stevensonii* were all found in plant communities characterised by relatively dense shrub layers creating light-limited conditions above a usually sparse ground layer which would impose little below-ground competition (chapter 4). The roots of shrubs usually lie below the rooting zone of seedlings.

C. curta and *C. juncea* were characterised as colonisers of open sites (chapter 4), which typically show low levels of shoot competition. Root competition in such early successional habitats can be high, but is usually symmetrical, as plants establish simultaneously on newly created sites (Tilman 1988; Wilson 1988). As the level of asymmetric root competition, the aspect considered here, can be rated as low, *C. curta* and *C. juncea* were expected to show weak competitive responses to both shoot and root competition.

C. australis was characterised as ubiquitous species occurring over a wide range of different habitat types. Levels of shoot and root competition are likely to vary accordingly, depending on the structure and composition of the vegetation. The versatility of *C. australis*, therefore, suggested a strong competitive response regarding both mechanisms, root and shoot competition. *C. petriei*, which was included as an additional common species, is ecologically similar to *C. australis*. While *C. australis* occurs north of 45° S in the east of the South Island, *C. petriei* occupies similar habitats further south (Heenan 1996b).

For each competitive mechanism, the species separated into two groups with expected weak or strong competitive responses, respectively. In the shoot competition experiment the grassland, shrubland and ubiquitous species were expected to show strong responses, while the rock outcrop species and the colonisers were expected to show weak responses. In the root competition experiment, rock outcrop species, grassland species and ubiquitous species were expected to show strong responses, while scrub and shrubland species and colonisers were grouped together, expected to show weak responses.

These hypotheses were tested in two competition experiments to explore the possibility of predicting the vulnerability of species to competition from their habitat ecology. As most competition studies focus on correlations of competitive ability with species characteristics other than habitat ecology, additional species characteristics were included in the analysis. These were seed size (c.f. Grime and Jeffrey 1965; Augspurger 1984), dry matter production (c.f. Grime 1979; Tilman 1988), maximum height of adult plants (c.f. Gaudet and Keddy 1988), and the length of the vessel elements in the wood of the *Carmichaelia* species (c.f. Carlquist 1988; Heenan 1997b).

5.5 Methods

5.5.1 Measurement of Competitive Response

The competitive response of the species was measured by comparing the performance of plants in the presence of neighbours with their performance when growing alone (Freckleton and Watkinson 2000; Keddy 2001).

Using the 'no competition'-treatment as standard, I calculated the competitive response (CR) as

$$CR = 1 - \frac{(P_0 - P_C)}{X} \ ,$$

where P_0 was the performance of the plants without competition, P_C the performance with competition, and X was either P_0 or P_C, whichever was greater. This equation followed Wilson and Keddy (1986), Goldberg and Fleetwood (1987), Goldberg and Landa (1991), Grace (1995), and Keddy et al. (1998) with modifications as suggested by Markham and Chanway (1996; see also Davis et al. 1998).

The resulting values for competitive response ranged from 0 to 2, with a value of 1 indicating that competition was not effective. Values larger than 1 pointed towards facilitative effects on the seedlings by their neighbours, while values smaller than 1 showed a negative effect of the neighbour on the seedlings.

The competitive response was calculated based on seedling survival and final dry weight as performance variables, provided these variables were significantly affected by the competition treatments (otherwise response values cannot be interpreted). The response values were then used to rank the species in competitive response hierarchies, and their agreement with the hypotheses was investigated.

Competitive response values attained in experiments describe the relative competitive ability of the study species, when compared to each other under the same growing conditions. For this purpose, the competitive response rankings are likely to be reliable for a range of different neighbours as well as abiotic environments (Goldberg and Landa 1991; Campbell and Grime 1992; Keddy et al. 1998). However, such rankings do not allow predictions on the

establishment success of individual species in their habitats in the field, as the attained response values are tied to the experiment (Goldberg 1996).

5.5.2 Seed Provenance and Handling

The seeds were mostly collected from plants in the wild during summer 1999/2000 (Table 5.2). If possible, seeds for each species were collected from two different populations, spread over the range of the species, and within each population from at least ten different plants. As most of the studied *Carmichaelia* are rare or threatened species, I tried to minimise the impact of seed collection on the population dynamics by only taking a small portion (c. 5%) of the seeds present on any one plant (Pavlovic et al. 1992; Norton et al. 1994).

Table 5.2: Seed lots used for the competition experiments.

Species	Provenance	Grid reference	Collection date	Trial 1	Trial 2
C. astonii	Ward, Marlborough	P29 07- 29-	1/03/00	√	√
C. australis	Mackenzie Pass, Canterbury	I38 15- 65-	7/04/00	√	√
C. australis	Lake Lyndon Rd, Canterbury	K35 0 -- 6 --	30/03/00	√	√
C. crassicaule	Porters Pass, Canterbury	K35 08- 67-	14/04/00	√	√
C. crassicaule	Macraes Flat, Otago	I43 05- 24-	22/03/01		√
C. curta	Lake Aviemore, Canterbury	I40 9 -- 1 --	2/03/00	√	√
C. curta	Mt John, Tekapo, Canterbury	I37 06- 88-	29/02/00	√	√
C. hollowayi	Awahokomo, Canterbury	I40 02- 08-	4/04/00		√
C. hollowayi	Gards Rd, Waitaki Valley, Otago	I40 14- 97-	4/04/00		√
C. juncea	Welcome Flats, South Westland	H36 66- 25-	8/03/00	√	√
C. juncea	Fox River, South Westland	H35 68- 43-	10/03/00	√	√
C. kirkii	Benmore Range, Canterbury	H39 83- 43-	3/05/00	√	√
C. kirkii	Tone Valley, Marlborough	O30 4 -- 0 --	19/01/00	√	√
C. muritai	Seaview, Clifford Bay, Marlborough	P28 06- 50-	19/02/00	√	√
C. petriei	Nenthorn, Otago	I43 0 -- 2 --	7/04/00	√	
C. stevensonii	Cultivation (Christchurch)	M35	15/05/00	√	√
C. stevensonii	Cultivation (Renwick)	P28 79- 66-	17/05/00	√	√
C. vexillata	Pukaki-Ohau Canal, Canterbury	H38 68- 56-	4/02/00	√	√
C. vexillata	Balmoral Station, Tekapo, Canterbury	I37 04- 82-	2/05/00	√	√

The seeds of *C. astonii* were collected from a single population at Ward, as the other populations are remote, and could not be visited at the time of seed maturity. In trial 1, *C. crassicaule* and also *C. petriei* were only represented by one population due to limited availability of seeds. *C. petriei* was excluded from the second experiment. As the amount of *C. hollowayi* seed was very limited due to small population sizes, this species was only used in the second experiment. *C. juncea* seeds were collected from only eight plants in the Fox River population, as no further fruiting individuals were present at the time of collection. The

C. kirkii seeds collected in the Tone Valley were probably one year old at the time of collection. They appeared still to be on the plants from the previous season. *C. muritai* seeds were collected from the Seaview population, the only population known at the time. Also, the seeds were taken from only four plants, as the other adults in the population were either not available, as they were part of a seeding trial conducted by the Department of Conservation, or they were not accessible in the steep habitat. As I did not find any *C. stevensonii* seeds in the wild, seeds were collected from plants in cultivation. Two plants were located in gardens in Renwick and two plants at the University of Canterbury, Christchurch. The genetic provenances of these plants were unknown.

The seeds were cleaned from their pods and tested for dormancy by soaking them in water for eight hours. As is typical for many Fabaceae, mature *Carmichaelia* seeds show physical dormancy effected by an impermeable testa (Grüner and Heenan 2001). This characteristic was used as indicator that the collected seeds were mature and undamaged. Seeds that imbibed during the test were removed. The dormant seeds were stored dry in paper bags at room temperature until the start of the trials.

The seeds were then individually scarified by nicking the testa with a scalpel, put on moist filter paper (Whatman grade 1, 8.5 cm) in 9 cm petri dishes, and germinated in an incubator at 17°C without artificial lights. The manual scarification sometimes damaged the seedling, if the applied cut had been too deep. However, after 3-5 days the radicle or cotyledons had sufficiently emerged from the seed coat to allow healthy and undamaged seedlings to be recognised. Only these seedlings were then transferred into the pots in the glasshouse. Both experiments were performed at the glasshouse facilities of the Department of Plant and Microbial Sciences at the University of Canterbury, Christchurch, New Zealand.

5.5.3 Trial 1: Light Competition

5.5.3.1 Treatments

The first experiment aimed at assessing the relative tolerance of *Carmichaelia* species to shade by submitting seedlings of ten species (Table 5.2) to conditions of permanently reduced irradiance. Three levels of irradiance were used: ‘no shade’, ‘medium shade’, and ‘dark shade’, with 36, 16, and 6% of outside, unshaded irradiance, respectively. These light levels corresponded with conditions found in habitats ranging from open scrub to forest understorey (Bieleski 1959; Hollinger 1987; van Gardingen 1987; Mc Donald and Norton 1992), and were, therefore, below the levels encountered by most *Carmichaelia* species in the field.

In the ‘no shade’ treatment the pots stood uncovered on the benches in the glasshouse receiving the ambient light present (reduced to 36% of outside irradiance by glasshouse construction; Fig. 5.1). The two shade treatments were achieved by placing the plants under wooden frames (45 cm high) that were covered with shade cloth. Knitted shade cloth of two qualities was used (Donaghys Envirolex Supashade Green 48% and Donaghys Sarlon-Hortshade Black 80%). To supplement the ambient light in the glasshouse 400 W sodium lamps were used providing 16 hours of daylight (Fig. 5.1).

Fig. 5.1: Light competition trial. The wooden frames are covered with green (48%) and black (80%) shade cloth creating levels of 16 and 6% of ambient outside irradiance, respectively.

The spectral quality of the available light was likely to differ between the treatments due to the varying quality of the shade cloth. However, the achieved reduction in irradiance was of such a magnitude that it seemed legitimate to assume this latter factor to cause the main effect in the experiment.

5.5.3.2 Experimental Design and Layout

The experiment was set up in a split-plot design (Damon and Harvey 1987; Snedecor and Cochran 1989) with eight replicates (Fig. 5.2). The three light levels represented the main plot and were randomly arranged within each replicate. The ten species represented the

subplot, being randomly arranged within each shade treatment. In addition, the two provenances of each species were randomly placed as a nested factor within the species. Four individual plants were used as the elementary experimental unit in the trial.

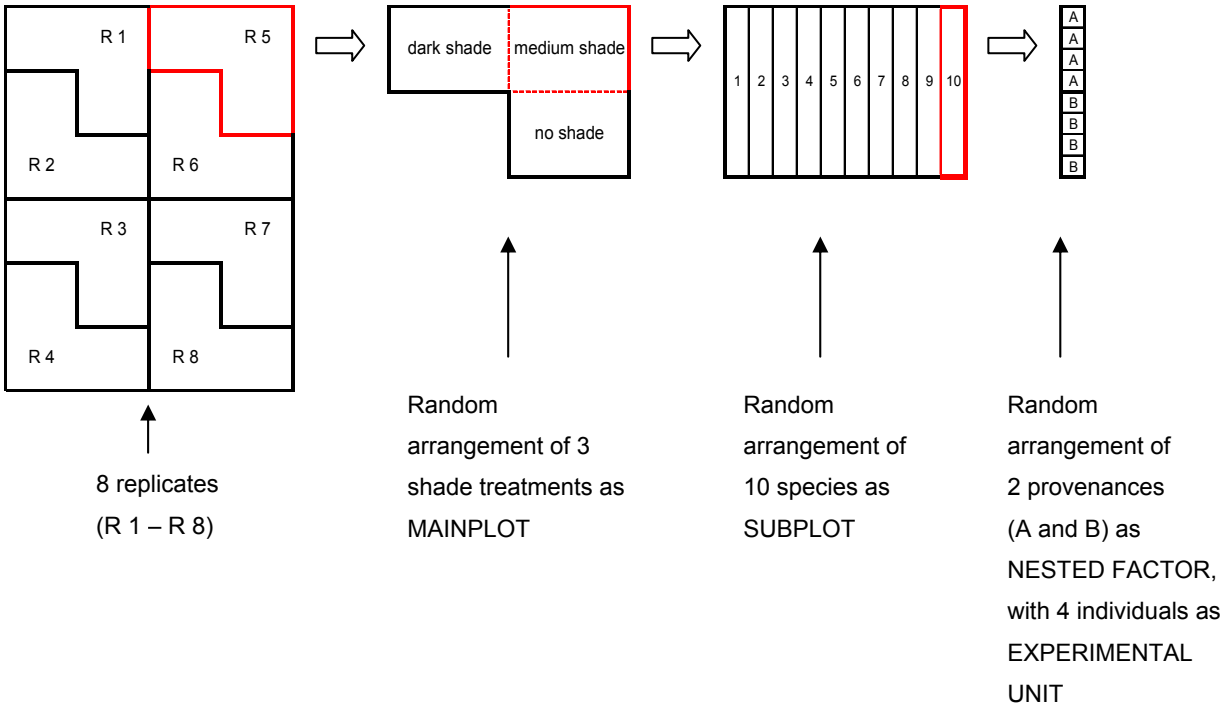


Fig. 5.2: Layout and experimental design of the light competition trial.

5.5.3.3 Timing and Procedures

Including the establishment and harvest periods, the experiment ran for 109 days from 1 September to 18 December 2000 (Fig. 5.3).

On 1 September 2000, young seedlings, prepared as described above (section 5.5.2), were pricked individually into 9 cm^2 pots (500 ml) filled with river sand. A paper square at the bottom of each pot prevented the sand from spilling when the pots were moved. For three weeks, the seedlings were left to establish under uniform glasshouse conditions and without the artificial lights, as the heat of the lights was likely to increase seedling mortality, which would have confounded the actual effect of competition for light. During this initial establishment period, dead plants were replaced with newly germinated seedlings. However, mortality was relatively low, and the plants were rearranged in such a way that no more than one replacement occurred in each experimental unit of four. When the treatments were implemented, on 21 September 2000, the largest age difference between seedlings was two weeks. A comparison of the shoot lengths ensured that there were no initial differences between the seedlings allocated to the three treatments (GLM, $p = 0.300$). To minimise

uncontrolled random effects due to location in the glasshouse, the benches were rotated fortnightly during the experiment.

5.5.3.4 Growing Conditions

Temperature and Relative Humidity

The temperature in the glasshouse was set at a minimum of 17°C, fluctuating above this level dependent on weather conditions. As the shade frames were expected to modify the microclimate of the shaded plots (Grime and Jeffrey 1965; Augspurger 1984; Williams and Buxton 1989), temperature and relative humidity were monitored during the experiment (see Appendix 4). The measurements showed that the plants without shade frames were subject to larger daily fluctuations than the shaded plots. During the day, temperatures were up to 6°C higher and relative humidity up to 15% lower, while at night, conditions were similar in all three treatments. Differences between the two shade treatments were relatively small. The variation in microclimate between the treatments could not be separated from the actual effect of competition for light. However, temperature and relative humidity are likely to vary in a similar manner in the field depending on the local light conditions.

Water

During the first three weeks of initial seedling establishment, the pots were head-watered daily. From the start of the actual trial period, watering was undertaken by flooding the benches every second day. When the roots of the largest plants began to grow out of the bottom of the pots, 67 days after pricking, the plants were again head-watered until the end of the trial. As the shade frames reduced evapotranspiration in the shaded plots, the open plots were selectively watered more often to keep soil moisture levels comparable between the treatments.

Fertiliser and Pesticides

Initially, the plants were grown without any addition of fertiliser. 48 days after pricking a slow release fertiliser (Plantacote pluss 4M, 14-9-15 + 2MgO + trace elements) was applied with 1.5 g per pot. The pots were head-watered the following two days, and from then on weekly, in order to wash the fertiliser into the substrate and prevent salination of the top layer. A pyrethrum-based insecticide was applied two weeks before harvest, as aphids were observed on some of the plants.

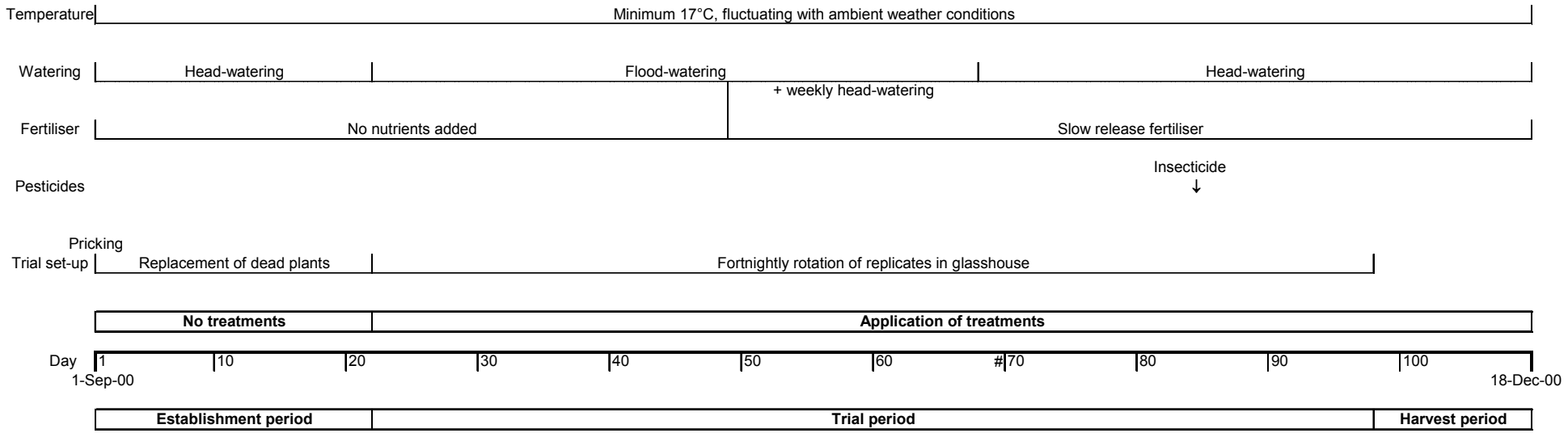


Fig. 5.3: Overview over the timing and procedures of the light competition trial.

5.5.3.5 Data Collection and Analysis

Mortality of seedlings was recorded fortnightly throughout the experiment. When the first individuals had converted to their adult growth form, 97 days after pricking, the plants were harvested (roots and shoots), dried to constant mass at 80°C, and weighed.

I used the statistical software package SAS 8.01 (SAS Institute Inc.) for all statistical data analyses. The significance level was chosen at $\alpha = 0.05$. The data for the final dry weight of the seedlings were ln-transformed prior to analysis to comply with the assumptions of normality, homoscedastity, and additivity.

The split-plot design used provided no actual replication, as the 'replicates' were arranged in blocks and included in the analysis as a random factor. Therefore, statistical tests required the interactions with the replicates to be zero to make them valid (those that use 'subplot errors') or interpretable (all tests) (Underwood 1997). This condition was met for the subplot error in all analyses. Where the mainplot error was significant, interpretation of results was still deemed appropriate, as the treatment effects were considerably larger.

First, the survival and dry matter data were analysed for significant effects of the shade treatments. This was done in a contingency table for the survival data (Fisher's exact test), and with ANOVA (GLM-procedure) for dry weight (ln-transformed data). The analysis of the dry weight data included only material from live plants.

When a significant effect of the shade treatments was found, the competitive response was calculated based on the respective variable, and with the 'no shade' treatment as standard. Differences between the species and between the provenances were analysed with ANOVA (GLM). The species were ranked in competitive response hierarchies according to their CR values, and the initial hypotheses were tested using linear contrasts.

Correlations with other species characteristics were examined using Pearson's product-moment correlation. Data on seed size and the maximum height of adult plants were obtained from Purdie (1985) and Heenan (1995, 1996b, 1998b). The final dry weight of the plants in the 'no shade' treatment was assumed to reflect the relative growth rate of the individual species, as all plants were grown over the same period of time from relatively small seeds.

5.5.4 Trial 2: Root Competition

5.5.4.1 Treatments

The root competition trial was set up as a target-neighbour experiment (Goldberg and Fleetwood 1987; Gibson et al. 1999) with seedlings of ten *Carmichaelia* species as targets (Table 5.2) grown individually with an established sward of *Agrostis capillaris* as neighbour. *Agrostis capillaris* is a widespread, introduced grass in New Zealand, and occurs at many *Carmichaelia* sites (chapter 4). Only one density of *Agrostis capillaris* was implemented, and the performance of the seedlings with this neighbour was compared to their performance without (Fig. 5.4).

As the grass sward was established from seed only four weeks prior to the experiment, the grass root density increased throughout the trial period. However, as the *Carmichaelia* seedlings were considered unlikely to have competitive effects on the grass, the density of grass roots was assumed to be equal in all pots throughout the experiment. The final grass root density was measured as 3.1 ± 0.45 g dry matter / litre substrate at harvest. Above-ground, the grass sward was kept short (5-7 mm) by regular clipping throughout the trial to minimise the occurrence of light competition.

Fig. 5.4: Root competition trial. Seedlings grown with and without *Agrostis capillaris* as competing neighbour.

5.5.4.2 Experimental Design and Layout

Similar to the light competition trial, the treatments (grass and no grass) and species were arranged in a split-plot design (Damon and Harvey 1987; Snedecor and Cochran 1989) with 8 replicates, and the provenances nested within the species (Fig. 5.5). Four individual plants were used as the elementary experimental unit in the trial.

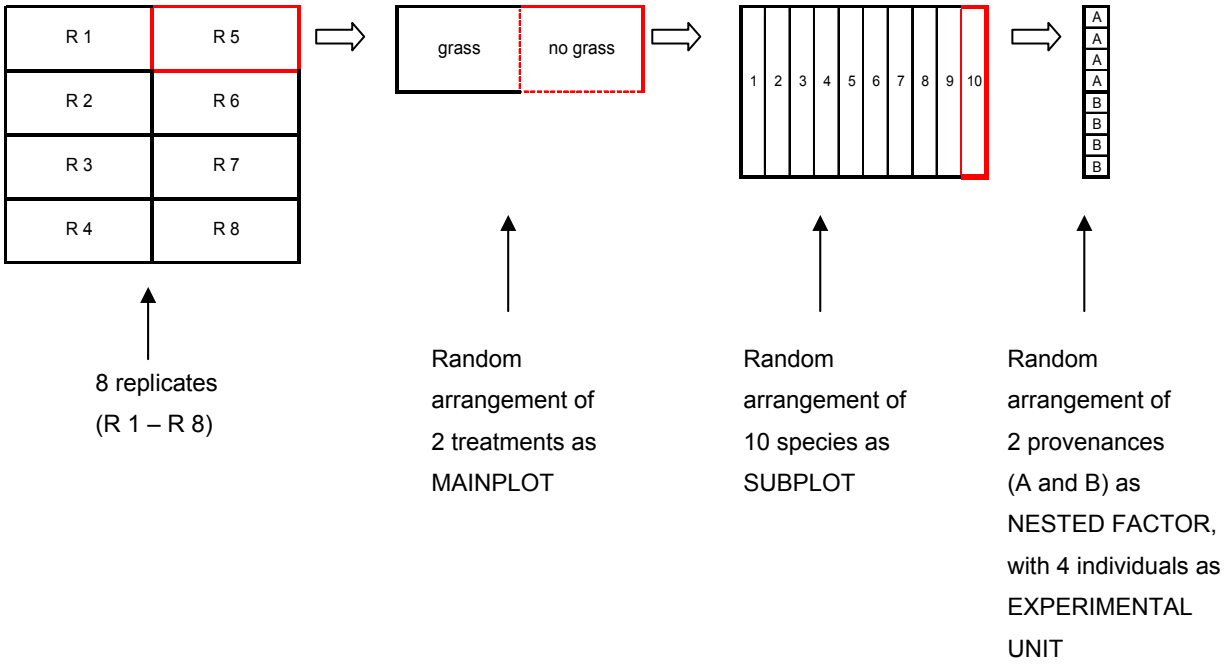


Fig. 5.5: Layout and experimental design of the root competition trial.

5.5.4.3 Timing and Procedures

Including the establishment and harvest periods, the experiment ran for 158 days from 22 June to 28 November 2001 (Fig. 5.6). On 22 June 2001, 9 cm^2 (500 ml) pots were filled with river sand, and *Agrostis capillaris* seed was evenly sown into half of them at 0.1 g / pot . A paper square at the bottom of each pot prevented sand from spilling when the pots were moved. All pots were watered regularly from above, and after 18 days, a liquid fertiliser and fungicide (see below) were applied. After 25 days, the grass was clipped back to 5-7 mm in length, and young *Carmichaelia* seedlings, prepared as described above (section 5.5.2), were pricked individually into the middle of each pot. A surplus of pots was prepared for each treatment to allow for mortality due to transplanting. Seven days later, the actual experimental period started, with establishment of the random set-up. All pots included in the trial contained live and healthy-looking seedlings. The replicates were rotated fortnightly throughout the trial to minimise uncontrolled effects due to location in the glasshouse.

5.5.4.4 Growing Conditions

Light

One week after the start of the experiment, 400 W - sodium lights were turned on, with a 16/8 hour light/dark cycle, to supplement the ambient irradiance in the glasshouse. An overall fluence rate of 60% of outside, unshaded irradiance was achieved. This level was higher than in the light competition trial, due to the different construction of the glasshouse.

Temperature

The temperature in the glasshouse was set at a minimum of 20°C, fluctuating above this level dependent on the weather conditions. On hot and sunny days temperature maxima of 30-35°C were recorded.

Water

Initially, the pots were regularly watered from above, to ensure good establishment of the grasses and young seedlings. During the trial period, pots were watered by flooding the benches, and the watering regime aimed at providing sufficient water supply for the seedlings grown without competition. Initially, this required flooding every 4-5 days, and later every 2-3 days, when plants became larger and the weather warmer.

Fertiliser and Pesticides

A liquid fertiliser (Yates Thrive 15-4-26 + trace elements) was applied at monthly intervals. As the dense grass sward increased the risk of fungal infection, a fungicide (Yates Greenguard) with chlorothalonil and thiophanate-methyl as active substances was applied fortnightly throughout the experiments. A pyrethrum-based insecticide was applied two weeks before harvest, as a small number of aphids were observed on several plants.

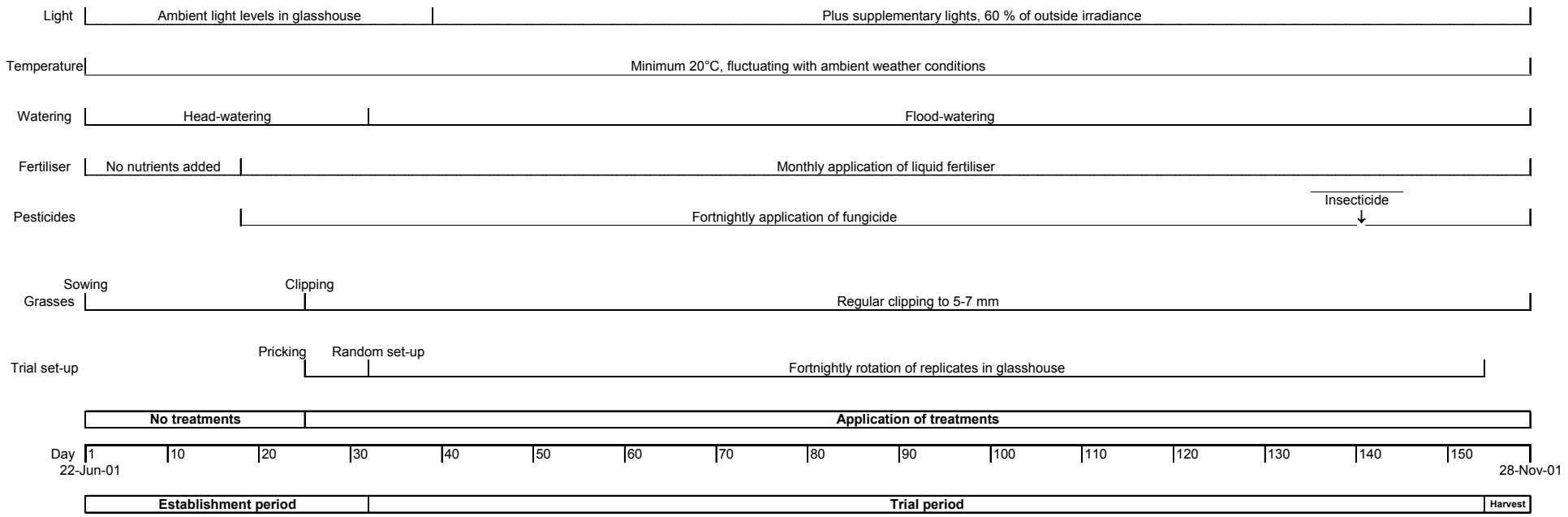


Fig. 5.6: Overview over the timing and procedures of the root competition trial.

5.5.4.5 Data Collection and Analysis

During the experiment, mortality of seedlings was recorded monthly. As in trial 1, the experiment ended, when the first individuals converted to their adult growth form. As the roots of the seedlings could not be separated from the dense mat of grass roots, only above ground biomass was harvested, dried to constant mass at 80°C, and weighed.

Analyses were performed as described for the light competition trial. The competitive response data based on shoot dry weight were ln-transformed before analysis. In addition to correlation analyses with Pearson's product-moment correlation, Spearman's rank correlation was used to examine the relationships between the two competitive response rankings based on survival and final dry weight and between these and the length of vessel elements. The ranking for the latter was obtained from Heenan (1997b).

The relationship between the responses to root competition on the one hand, and shoot competition on the other, was examined with Spearman's rank correlation, using the data of the nine species that were part of both experiments.

5.6 Results

5.6.1 Trial 1: Light Competition

5.6.1.1 Effects on Survival

The shade treatments showed no significant effect on the survival of the seedlings (Fisher's exact, $p = 0.697$; Fig. 5.7). While for some species seedling mortality increased with decreasing light levels, other species showed the opposite or no trend, but variability was too high to show significant patterns.

Overall, the seedlings of *C. muritai* suffered the highest mortality, with 31% dead plants in the dark shade treatment, while most seedlings of *C. crassicaule* and *C. kirkii* survived until the end of the experiment.

5.6.1.2 Effects on Final Dry Weight

In contrast to their effect on survival, the effect of the shade treatments on dry matter production was very pronounced ($p < 0.001$; Fig. 5.8). The final dry weight of the trial plants decreased with decreasing light levels for all species, although their maximum productivity

differed widely. *C. kirkii* plants, for example, produced over 500 mg of dry matter in the 'no shade' treatment, compared to just 58 g produced by *C. muritai*.

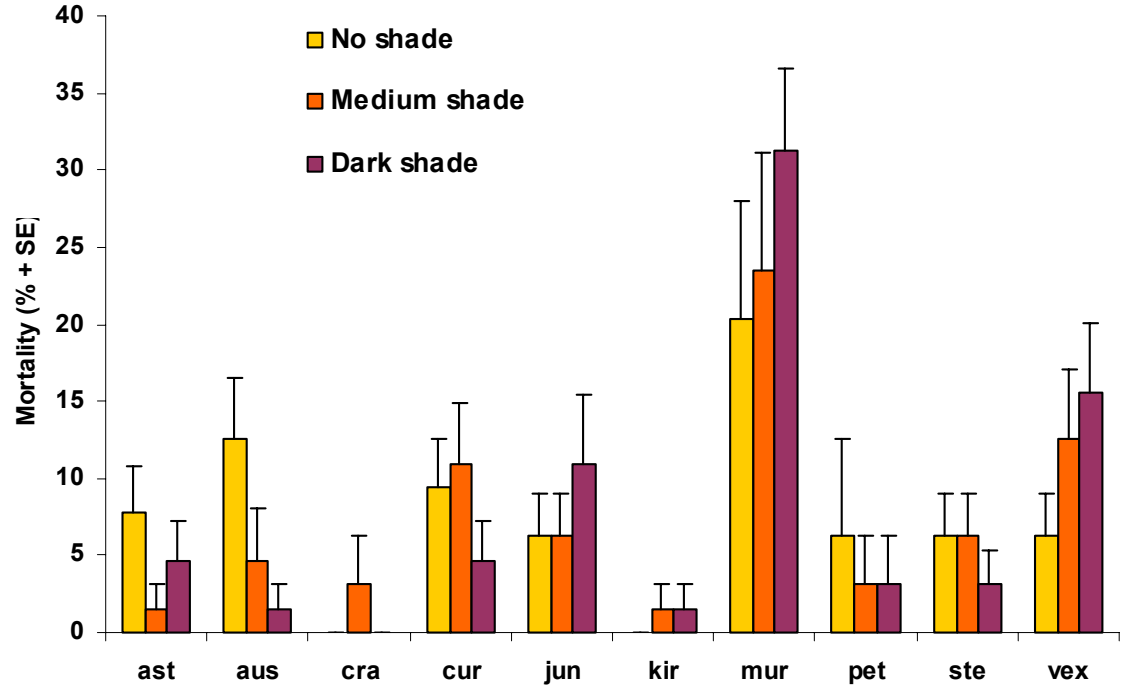


Fig. 5.7: Mortality of the *Carmichaelia* seedlings in the three shade treatments. ast - *C. astonii*, aus - *C. australis*, cra - *C. crassicaule*, cur - *C. curta*, jun - *C. juncea*, kir - *C. kirkii*, mur - *C. muritai*, pet - *C. petriei*, ste - *C. stevensonii*, vex - *C. vexillata*.

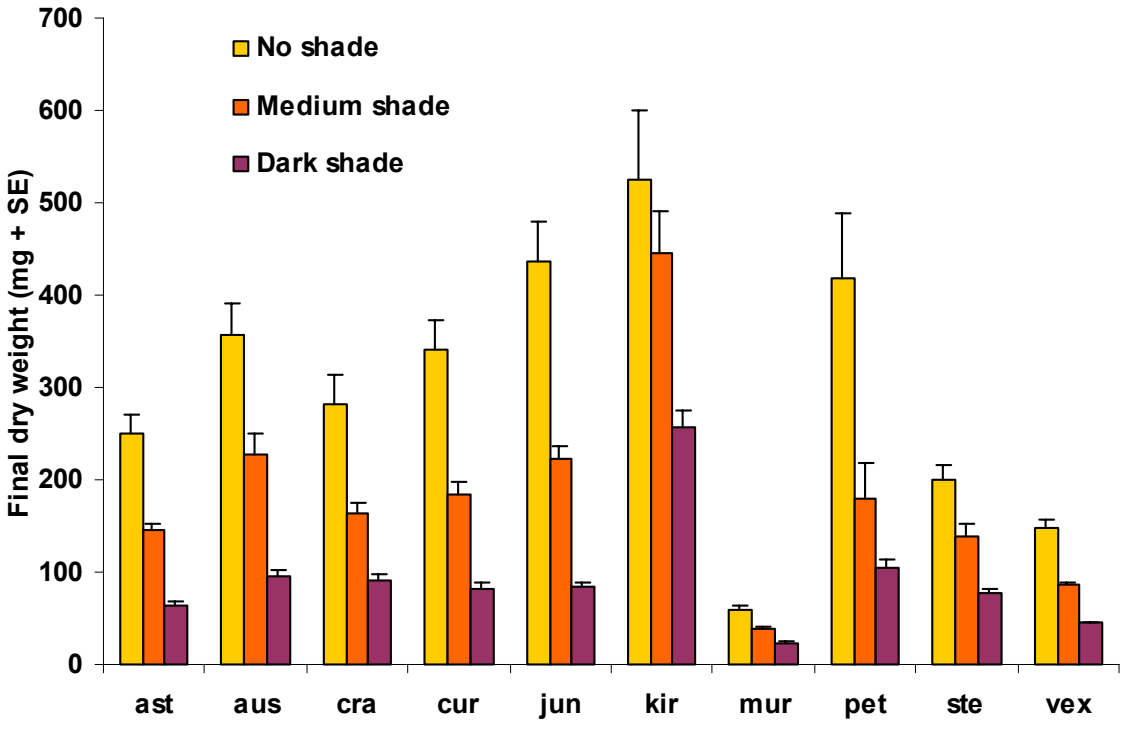


Fig. 5.8: Final dry weight of the *Carmichaelia* seedlings in the three shade treatments.

5.6.1.3 Competitive Response Based on Final Dry Weight

As the effect of the shade treatments on seedling mortality was not significant, the competitive response of the species was only calculated based on the final dry weight of the plants.

An ANOVA of the attained response values showed that the strongest effect was clearly caused by the shade treatments (Table 5.3), and although the interaction with the replicates (Error term) was significant, the results were still considered interpretable because of the magnitude of the shade effect. The weak effect caused by the replicates justified the chosen blocked design of the experiment. In the subplot analysis, differences between the species also proved to be highly significant, and furthermore, were independent of the shade effect. This allowed the species to be compared and ranked according to their mean competitive response in the two shade treatments. Differences between the two provenances of each species were not apparent.

The mean competitive response of the species ranged from 0.38 for *C. petriei* to 0.77 for *C. kirkii*, and the ranking of the other species between these two extremes was surprisingly consistent with the hypothesised competitive responses (Fig. 5.9). Linear contrasts separated the grassland (*C. crassicaule*, *C. vexillata*), shrubland (*C. kirkii*, *C. muritai*, *C. stevensonii*), and ubiquitous species (*C. australis*, *C. petriei*), which were all expected to show strong responses, from the colonisers (*C. curta*, *C. juncea*) and rock outcrop species (*C. astonii*) ($F = 28.74$, $p < 0.001$). Furthermore, the ecological groups themselves appeared ranked in their competitive responses. The three scrub and shrubland species showed the strongest responses, followed by the two grassland species. The colonisers, *C. juncea* and *C. curta* ranked at the lower end, together with *C. astonii* as rock outcrop species. Only the ubiquitous species were not grouped together, with *C. petriei* showing the weakest response of all species, and *C. australis* ranking in the middle. Linear contrasts separated the three shrubland species from the rest ($p < 0.001$). Furthermore, the response of *C. kirkii* was significantly stronger than that of *C. muritai* and *C. stevensonii* ($p < 0.001$). Differences between the other ecological groups were not significant ($p = 0.996$).

Table 5.3: Effects of replicates (rep), shade, species, and provenance (prov) on the competitive response based on the final dry weight of the plants.

Source	DF	F-Value	Pr > F
Main plot			
rep	7	3.93	0.046
shade	1	80.73	<0.001
Error (rep * shade)	7	3.09	0.005
Subplot			
species	8	12.30	<0.001
shade * species	8	0.52	0.842
Error (rep * species (shade))	112	1.32	0.064
Subsubplot (nested)			
prov (species)	9	1.77	0.081
shade * prov (species)	9	0.78	0.639

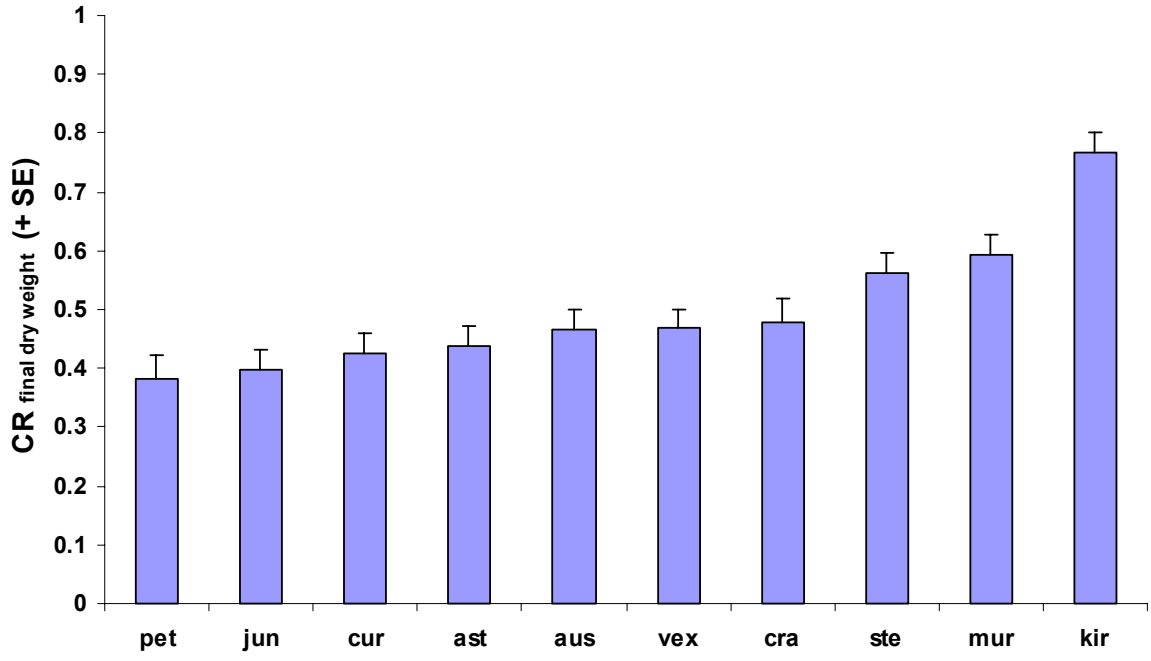


Fig. 5.9: Mean competitive response (CR) of the *Carmichaelia* species to light competition.

5.6.1.4 Correlations between Competitive Response and Other Species Characteristics

While the competitive response based on final dry weight was not significantly related to seed size, a negative correlation with the productivity of the seedlings, when growing without competition, was apparent (Fig. 5.10). The high response values of C. *muritai* and *C. stevensonii* were associated with relatively low final dry weights in the 'no shade' treatment, while the species with weaker competitive responses showed higher productivity. *C. kirkii* was as an outlier in this relationship, showing the highest productivity as well as the strongest competitive response of all species studied. Accordingly, the correlation was only statistically significant, if *C. kirkii* was excluded from the analysis ($p = 0.953$ vs. $p = 0.004$).

A similar pattern emerged in the analysis of the correlation between competitive response and the maximum height of adult plants of the various species. These two variables were positively correlated, with a significant relationship (p = 0.008), if *C. kirkii* was excluded. Furthermore, this correlation was mainly driven by the two tall growing species, *C. muritai* and *C. stevensonii*, as an analysis including only the small and medium sized species was not significant (p = 0.856).

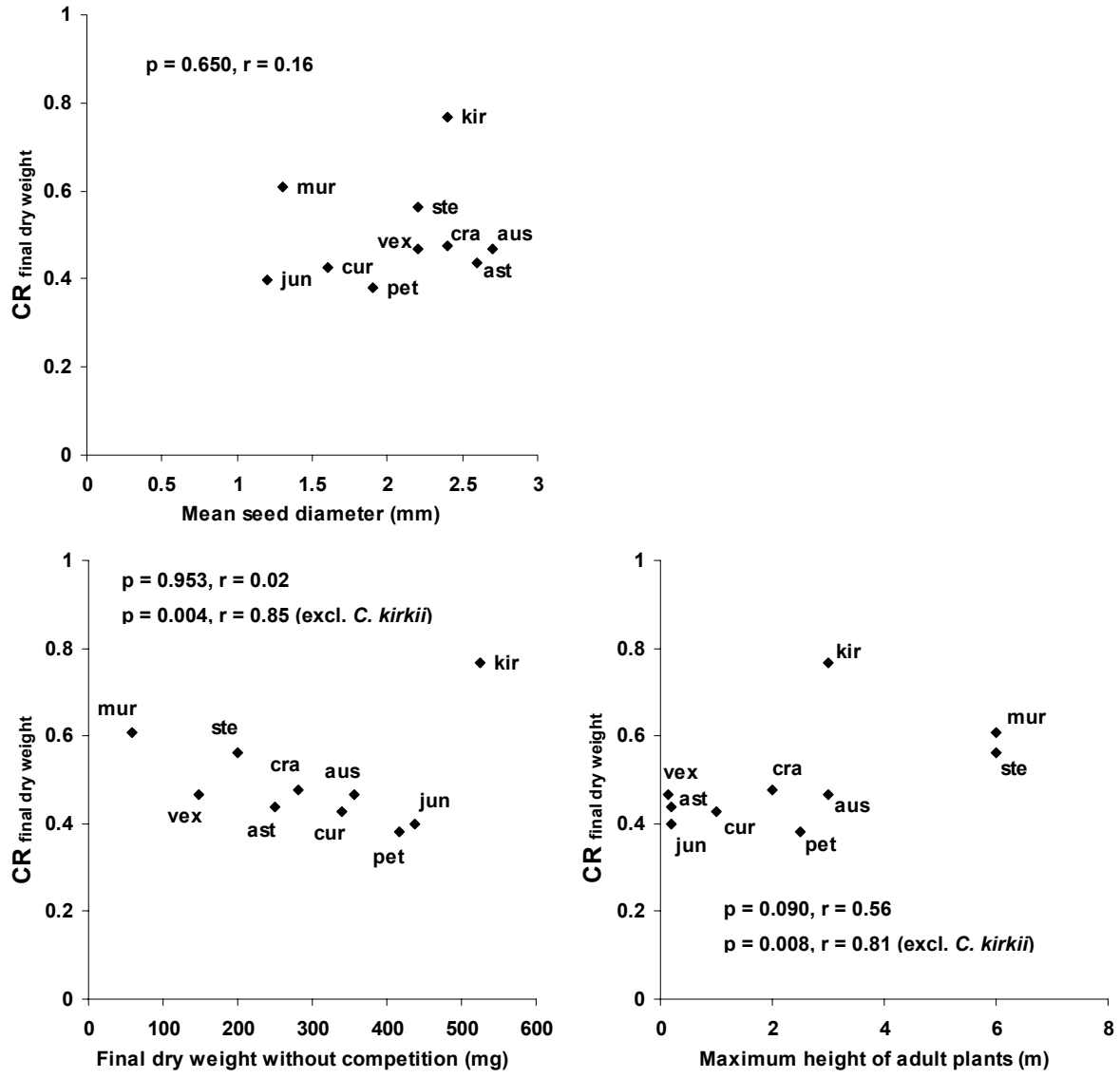


Fig. 5.10: Correlation between the competitive response (CR) of the *Carmichaelia* seedlings to light competition and seed size, dry matter production, and maximum height of adult plants.

5.6.2 Trial 2: Root Competition

5.6.2.1 Effects on Survival

Root competition had a significant effect on the survival of the seedlings ($p = 0.004$; Fig. 5.11). Most of the species suffered higher mortality in the presence of the grass sward. However, *C. australis*, *C. curta*, and *C. kirkii* showed the opposite trend.

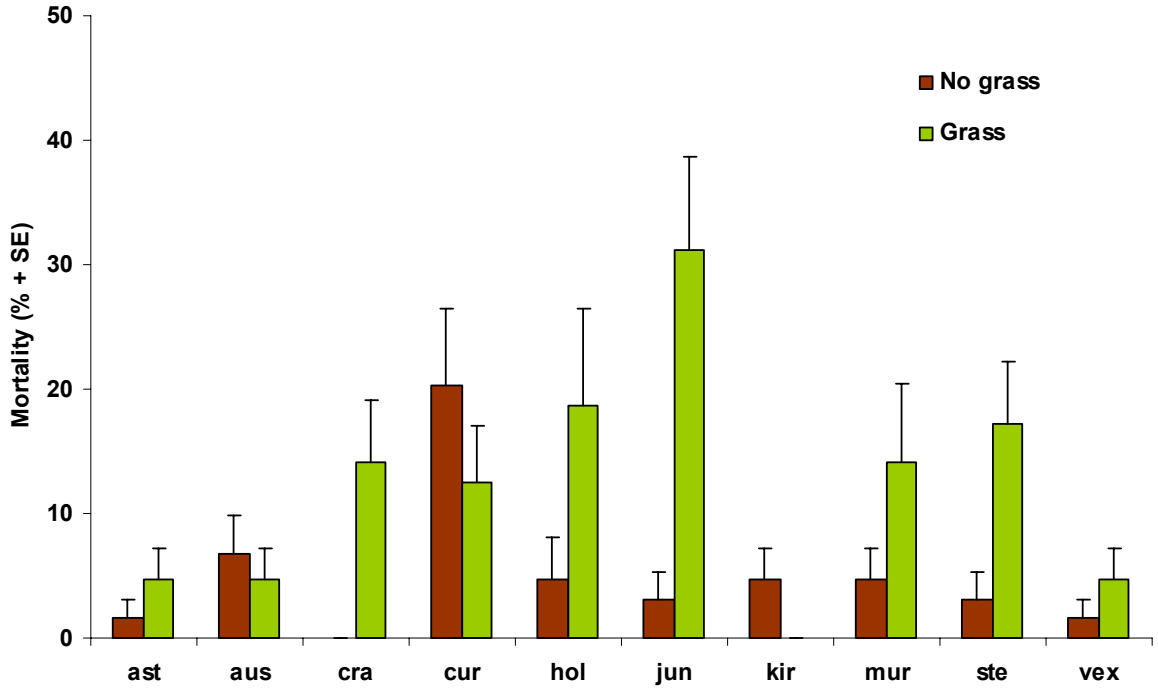


Fig. 5.11: Mortality of the *Carmichaelia* seedlings in the root competition experiment.

5.6.2.2 Effects on Final Dry Weight

Dry matter production was drastically reduced for all ten study species in the grass treatment (Fig. 5.12). The effect was of such a magnitude that statistical tests became unnecessary. None of the species produced more than 40 mg of above ground dry matter per plant when growing with the grass sward. Without competition, the species varied widely in their overall productivity, with *C. australis* being the most productive (391 ± 34.2 mg) and *C. muritai* the least (94 ± 6.0 mg).

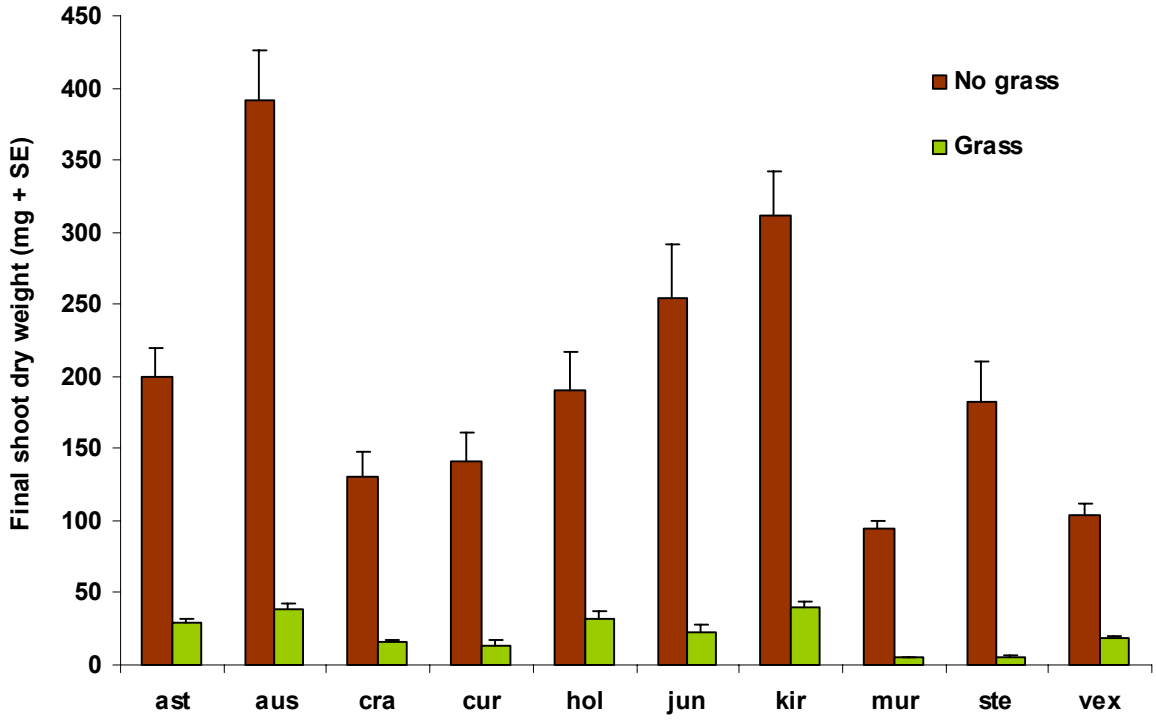


Fig. 5.12: Final shoot dry weight of the *Carmichaelia* seedlings in the root competition experiment.

5.6.2.3 Competitive Response Based on Survival

The competitive response based on survival showed significant differences between the species, but not between the provenances (Table 5.4). The replicates had no significant effect on the response in this experiment.

Table 5.4: Effects of replicates (rep), species, and provenance (prov) on the competitive response of the species based on survival.

Source	DF	F-Value	Pr > F
Mainplot			
rep	7	0.46	0.861
species	9	4.83	<0.001
Error (rep * species)	63	0.80	0.816
Subplot (nested)			
prov (species)	10	1.78	0.081

Overall, the competitive response of the study species seemed relatively strong, as most of the species showed values close to 1 (Fig. 5.13). *C. juncea* expressed the weakest response with a 30% increase in mortality compared to the 'no grass'-treatment. Differences in the competitive ability of the species according to the initial hypotheses were not apparent ($p = 0.628$), and the ranking did not reflect the habitat characteristics of the species. Instead, the colonisers *C. juncea* and *C. curta* ranked at either end of the hierarchy, and no pattern in the arrangement of the other species was apparent.

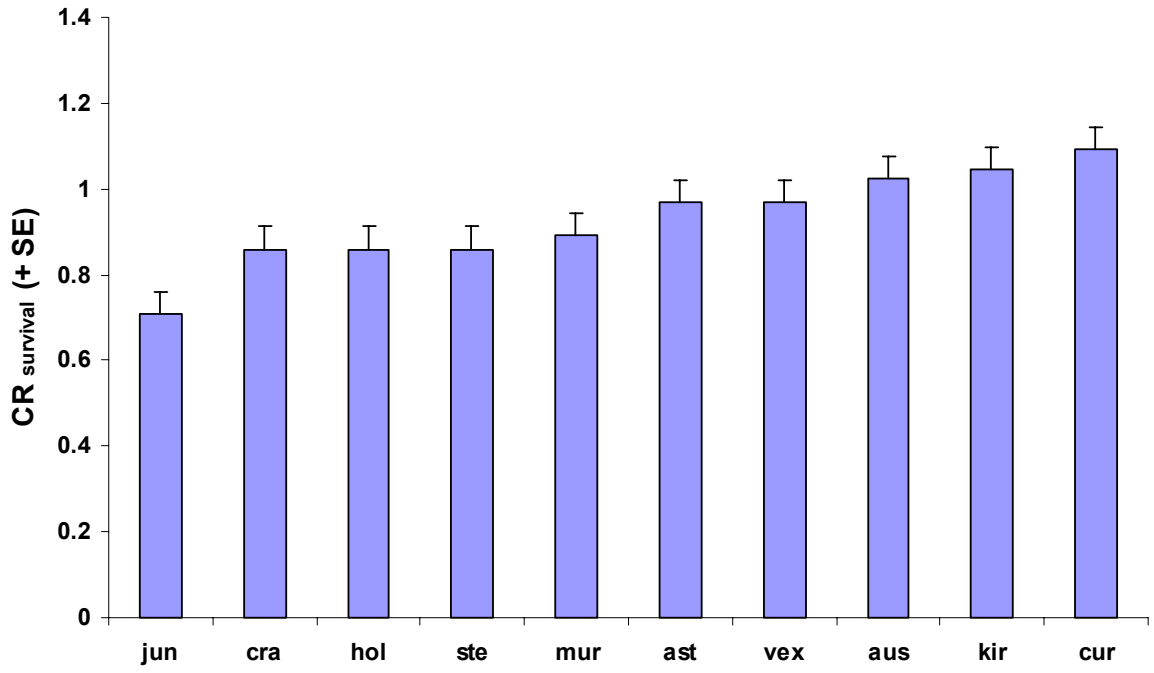


Fig. 5.13: Competitive response (CR) of the *Carmichaelia* species to root competition, based on survival.

5.6.2.4 Competitive Response Based on Final Dry Weight

Similar to the response based on survival, differences in the competitive response based on final dry weight were evident between the species, while the provenances showed no significant effect (Table 5.5).

Table 5.5: Effect of replicates (rep), species, and provenances (prov) on the competitive response to root competition, based on final shoot dry weight.

Source	DF	F-Value	Pr > F
Mainplot			
rep	7	1.74	0.117
species	9	3.27	0.003
Error (rep * species)	63	0.91	0.653
Subplot (nested)			
prov (species)	10	1.89	0.061

The competitive response values were very low for all species, due to the strong impact of the grass treatment on the plants. *C. hollowayi* showed the strongest response with a value of 0.24. *C. stevensonii* and *C. muritai* ranked at the lower end with response values of 0.04 and 0.05, respectively.

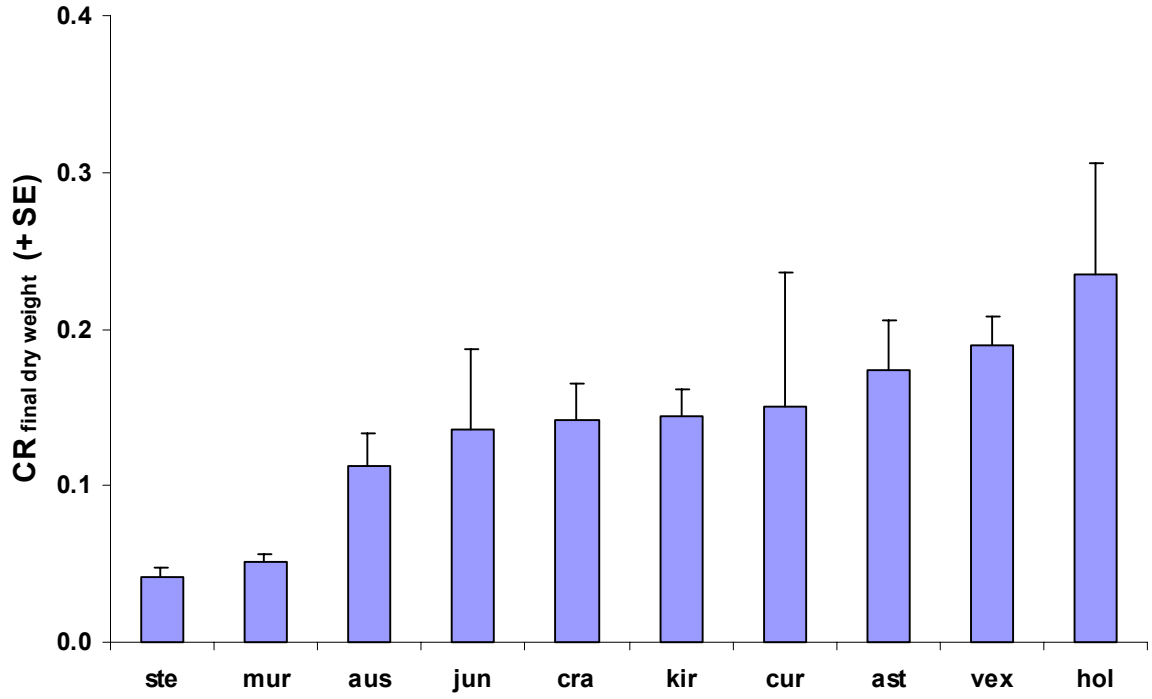


Fig. 5.14: Competitive response (CR) of *Carmichaelia* species to root competition, based on final shoot dry weight.

Linear contrasts showed significant differences between the species expected to express strong and weak responses, respectively ($p = 0.001$, $F = 12.62$). However, the ranking of the species corresponded only partly with the hypotheses. As expected, *C. stevensonii* and *C. muritai* ranked low, but *C. kirkii* and *C. curta*, also expected to show weak responses, ranked relatively high. Similarly, *C. astonii*, *C. vexillata*, and *C. hollowayi* ranked high, meeting the hypotheses, but *C. australis* and *C. crassicaule* ranked comparatively low. Consequently, differences between the ecological groups were not significant ($p = 0.051$, $F = 3.94$). However, *C. muritai* and *C. stevensonii* separated significantly from all other species ($p < 0.001$, $F = 20.32$).

5.6.2.5 Survival versus Final Dry Weight as Response Variable

The competitive response based on final dry weight was not only considerably weaker than the response based on survival, but the resulting hierarchies also showed distinct differences (Fig. 5.15). Some species, e.g., *C. juncea* and *C. hollowayi*, ranked considerably lower in their response based on survival than they did with respect to final dry weight, while other species showed the opposite trend (e.g., *C. australis*). The correlation between the two response hierarchies was not significant ($p = 0.538$, $r = 0.22$).

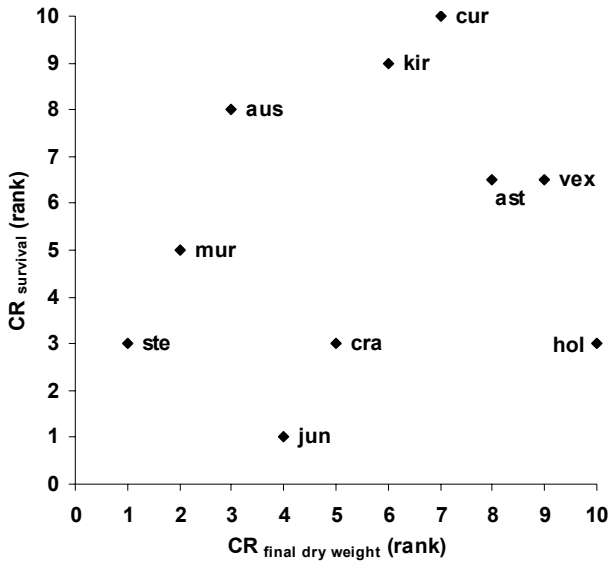


Fig. 5.15: Correlation between the competitive response (CR) rankings based on survival and final shoot dry weight.

5.6.2.6 Correlations between Competitive Response and Other Species Characteristics

The competitive response of the *Carmichaelia* species to root competition was not significantly correlated with seed size or plant productivity for either response variable (Fig. 5.16). The length of the vessel elements in the wood of *Carmichaelia* species was also not significantly related to the competitive response based on survival, but when based on final dry weight, a clear relationship emerged. The longer vessel elements of *C. stevensonii*, *C. muritai*, and *C. australis* were associated with lower response values, while species with shorter vessel elements showed stronger competitive responses.

5.6.3 Shoot Competition versus Root Competition

Although the *Carmichaelia* species showed varying vulnerability to both components of competition, root competition clearly had the more severe impact on the seedlings. The growth of the plants was far more inhibited in the grass treatment than in the dark shade treatment.

The ranking of the species in their response to root and shoot competition differed considerably. Correlations between the attained response rankings were not apparent (Fig. 5.17). While some of the species showed inverse relationships with a strong response to one competitive mechanism and a weak response to the other (*C. muritai*, *C. stevensonii*, *C. curta*), others ranked consistently high (*C. kirkii*) or relatively low (*C. juncea*) in all three hierarchies.

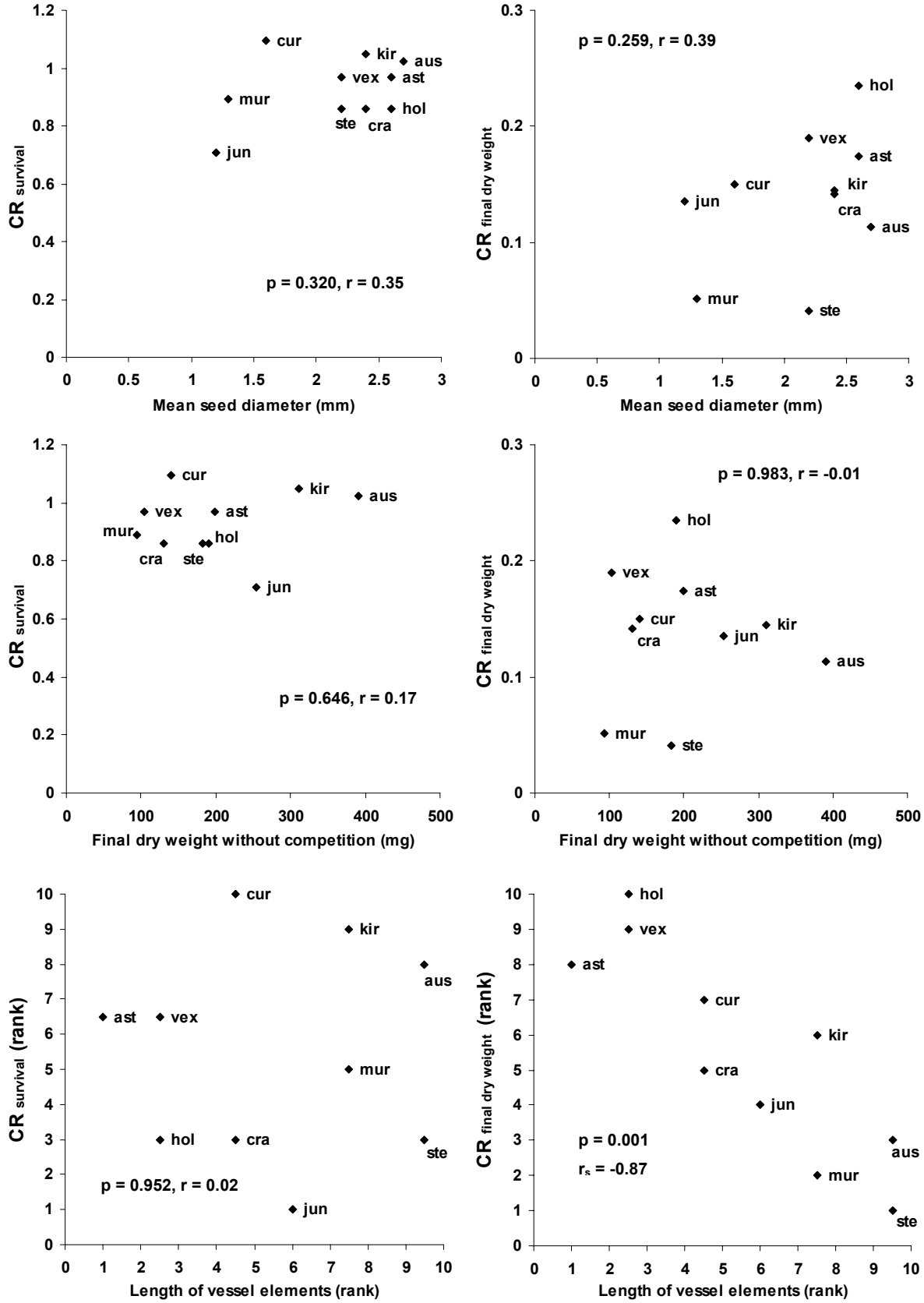


Fig. 5.16: Correlation between the competitive response (CR) of the *Carmichaelia* seedlings to root competition and seed size, dry matter production, and length of vessel elements.

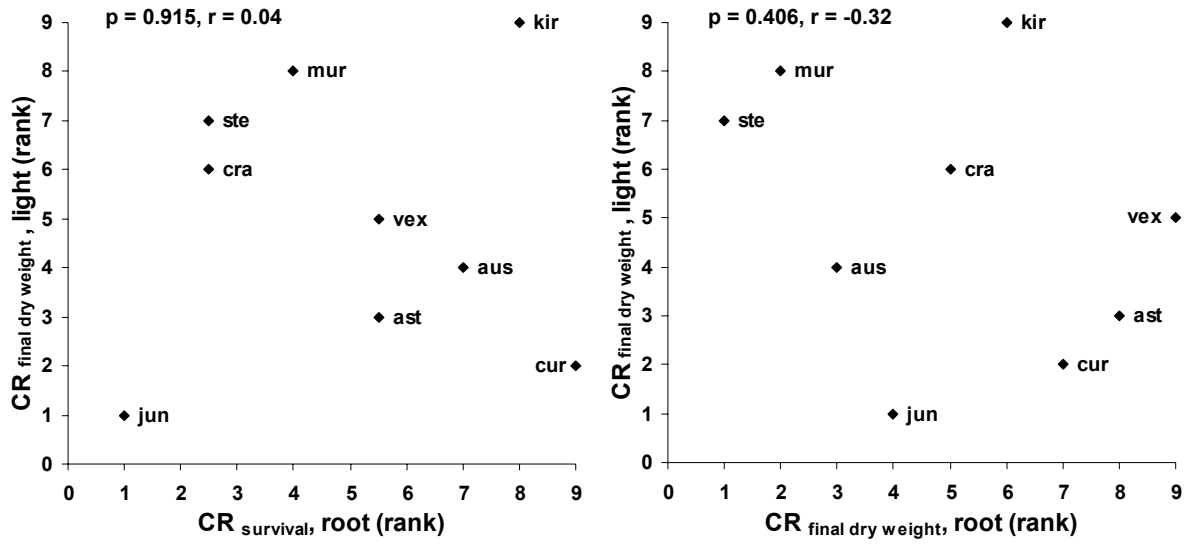


Fig. 5.17: Correlation between the competitive responses (CR) to competition for light and root competition.

5.7 Discussion

The impact of introduced species on native plants is likely to vary depending on the relative adaptation of the latter to competitive growing conditions (Keddy 2001). The results presented here, demonstrated that it is possible to predict, which species are likely to be more vulnerable to competition than others, based on the characteristics of their habitats. However, the hypotheses were only met when final dry weight was used as response variable for competitive response.

5.7.1 Survival versus Final Dry Weight as Response Variable

While the species showed clear differences in their vulnerability to competition, when final dry weight was used as variable for competitive response, all *Carmichaelia* species appeared to be relatively tolerant to both, shoot and root competition, with respect to survival. The reduced irradiance in the shade treatments did not lead to a consistent increase in plant mortality, although the light levels used were very low compared with those in the natural habitats of most species. In the root competition experiment, only *C. juncea* was strongly affected.

The differences in the two response rankings based on survival and final dry weight highlighted that species differ in which variable or life stage makes them most vulnerable to competition, and that different variables need to be considered to fully understand the effects of competition on a species (Howard and Goldberg 2001). For example, in the root competition experiment, *C. juncea* was the most vulnerable species with regard to survival, but occupied an intermediate position in its response based on final dry weight. The biological significance of the impact of competition on seedling mortality for this species needs further clarification.

The overall relatively weak effect of competition on seedling survival was consistent with findings by Howard and Goldberg (2001). Their study shows, furthermore, that competitive response based on survival represents a weak indicator for the actual success of species in a plant community. Competitive response values based on variables describing plant growth, in contrast, correlate well with the abundance of species in their habitats (Howard and Goldberg 2001). According to these findings, the hypotheses established in this study predicted, in fact, the relative ability of the various *Carmichaelia* species to persist under competitive growing conditions, as they predicted the competitive response based on final dry weight, a variable describing plant growth (but see Aarssen and Keogh 2002). Such estimates on the likely persistence of species under the impact of competition are of high interest for the conservation management of threatened species.

5.7.2 Trial 1: Light Competition

In the light competition experiment, the hypotheses were not only supported by linear contrasts, but in addition, the attained competitive response ranking established a sequence of vulnerability relating to the ecological grouping of the species.

The scrub and shrubland species clearly showed the strongest tolerance to light competition, separating significantly from the other species. *C. kirkii* appeared particularly adapted to this competitive mechanism, with its response being significantly stronger than that of *C. muritai* and *C. stevensonii*.

The shade tolerance of *C. stevensonii* is supported by findings that the chloroplasts of this species possess characteristics typical for shade tolerant plants (Riach 1995). However, a controversy arises from the fact that *C. muritai* and *C. stevensonii* have upright, monopodial juveniles (Heenan 1997a). This growth habit has been described as typical for light demanding plants, as an adaptation that allows seedlings to rapidly grow above the height of

possible competitors (Grime 1979). However, *C. stevensonii* and, in particular, *C. muritai* showed relatively slow height growth in both experiments, and as the transition from juvenile to adult form occurs with adults stems emerging from the base of the plants rather from the top (Heenan 1997a), the monopodial growth of the juveniles of these species does not appear to be an adaptation to light competition.

The grassland species ranked next to the scrub and shrubland species, supporting the hypothesis that they are also relatively well adapted to competition for light, while, as expected, the colonisers and rock outcrop species ranked low, being vulnerable to shoot competition. The lack of statistically significant differences between these groups could be caused by the hypotheses overestimating the level of light competition in tall tussock grassland. Furthermore, the results would possibly have been more conclusive if a true 'full light' treatment had been used as control, as due to the construction of the glasshouse, the 'no shade' treatment provided only 36% of ambient outside irradiance.

The ubiquitous species *C. petriei* and *C. australis* ranked amongst the more vulnerable species, although in chapter 4, *C. australis* was characterised as showing a preference for scrub and shrubland habitat, and the same is likely to be true for *C. petriei* (Heenan 1996b). The relatively high vulnerability of these species to light competition implied that they are likely to prefer open scrub habitat, possibly benefiting from disturbance (see chapter 4).

5.7.3 Trial 2: Root Competition

In the root competition experiment, the relationship between the habitat of the species and their vulnerability to competition was not as clear as in the shoot competition trial. Although the linear contrasts comparing the species predicted to show weak or strong responses respectively, were significant, the ranking revealed that these predictions were only partially met.

As expected, the scrub and shrubland species *C. stevensonii* and *C. muritai* showed weak responses, being significantly more vulnerable than all other species, but *C. kirkii*, as the third scrub and shrubland species, was more tolerant to root competition than expected.

Although the differences between the ecological groups were not significant, the high ranks of *C. astonii*, and especially *C. hollowayi*, seemed to reflect their adaptation to the extreme competitive conditions of rock outcrop habitats (Keogh 2000, after Keddy 2001). Similarly, the performance of *C. vexillata* agreed with its characterisation as grassland species. In

addition, the seedlings of this species showed very fast initial height growth, a feature interpreted as a shade avoidance strategy typical for grassland species (Grime and Jeffrey 1965; Fenner 1978).

The other species ranked in the middle of the hierarchy, indicating stronger (*C. curta*, *C. juncea*) or weaker (*C. australis*, *C. crassicaule*) adaptation to root competition than expected. The habitat ecology of these species might not yet be fully understood, leading to erroneous hypotheses. However, as differences between the species were slight and variation high, further experiments would be needed to clarify any trends.

5.7.4 Correlations between Competitive Response and Other Species Characteristics

The observed correlations between the competitive responses and other characteristics of the *Carmichaelia* species supported the validity of the findings and provided insight into some of the mechanisms by which competition affected the performance of the seedlings.

Final Dry Weight

The correlation between the competitive responses of the species and their final dry weight when growing without competition was only significant with respect to light competition. This is consistent with findings in other competition studies, as, although this correlation has been put forward for the competitive ability of species in general (Grime 1979; Tilman 1988; Goldberg and Landa 1991), experimental evidence is restricted to the shade tolerance of species (Grime and Jeffrey 1965; Augspurger 1984; Williams and Buxton 1989; Ebbett and Ogden 1998). Keddy et al. (1998), who did not distinguish between above and below ground competition in their experiment, found no relationship. In the data presented here, a correlation with the response to root competition might have emerged, if root dry weight had been included in the analysis, as root competition is thought to specifically stimulate root growth (Keddy 2001).

A drawback for the correlation as it is presented in this study lies in the fact that the final dry weight of the plants was measured in the same experiment as the competitive response. Growth rates measured in the field would be needed to ensure the objectivity of the assessed correlations. The only observation in this respect, has been made by Williams et al. (1996) confirming the slow growth of *C. muritai* seedlings. However, the comparison of the study species across the two experiments showed that, although the experiments were

performed independently, the ranking of the species according to their productivity was similar (Spearman rank: $p = 0.007$, $r_S = 0.82$). This indicated that the experiments adequately reflected the productivity of the *Carmichaelia* species, at least when compared to each other.

Maximum Height

The strong correlation between the shade tolerance of the species and their maximum height as adult plants was consistent with findings by Gaudet and Keddy (1988), Keddy and Shipley (1989), and Freckleton and Watkinson (2001). The more shade tolerant, tall growing *C. muritai* and *C. stevensonii* stood distinctly apart from the other species. However, the results also indicated that this relationship is only valid, if the species included in the analysis cover a relatively wide range of sizes, as the correlation was not significant, when *C. muritai* and *C. stevensonii* were excluded.

The correlations of shade tolerance with final dry weight and maximum height, valid for the other *Carmichaelia* species, did not apply to *C. kirkii*. Although its shade tolerance was very pronounced, this species showed the highest dry matter production of all species studied. *C. kirkii* is the only climber within the genus, and its unusual performance in the experiments indicated that it follows a different life history strategy, typical for many climbing plants (Baars and Kelly 1996). Correlations of competitive ability with growth rate and plant size have been described for herbs, shrubs, and trees, but none of the studies mentioned above included climbing plants.

Seed Size

The competitive response of the *Carmichaelia* seedlings was not significantly related to seed size in both experiments. This correlation has been analysed with conflicting results in other studies. While Grime and Jeffrey (1965) and Gross (1984) reported a positive correlation, Augspurger (1984) found no relationship.

Length of Vessel Elements

The competitive response based on final dry weight, assessed in the root competition experiment, was strongly correlated with the length of the vessel elements of the *Carmichaelia* species. This suggested that the main mechanism with which the grasses affected the *Carmichaelia* seedlings was competition for soil water. Species of xeromorphic habitats develop narrow and short vessel elements in adaptation to drought conditions (Carlquist 1988). Although *Carmichaelia* are generally characterised by xeromorphic wood anatomy, they also show a gradient in their adaptation, the length of their vessel elements being one indicator (Heenan 1997b). The observed tolerance to root competition coincided

with this gradient of adaptation to drought. Grasses are known to be strong competitors, in particular for soil water (Goldberg and Fleetwood 1987; Gordon et al. 1989). With their dense and shallow root systems, they can affect the seedlings of trees and shrubs to a degree that successful regeneration is prevented (Gordon et al. 1989; Harrington 1991; D'Antonio and Vitousek 1992; Eliason and Allen 1997; Davis et al. 1998). Findings by Sessions and Kelly (2000) indicate such an effect for a number of New Zealand shrubs in competition with a sward of *Agrostis capillaris*, and the results presented here support this for the *Carmichaelia* species. However, competition for water seemed to only affect plant productivity, as the correlation with the competitive response based on survival was not significant.

Competition for nutrients was a second mechanism effective in the root competition experiment. Despite regular fertiliser applications, plants of *C. vexillata* showed a distinct orange colouring in the competition treatment. Caldwell et al. (1985, 1987) demonstrated strong active competition between grasses and shrubs for nutrient resources.

5.7.5 Competitive Ability as Species Characteristic

While the *Carmichaelia* species varied considerably in their relative vulnerability to the impact of competition, differences between the provenances of each species were not apparent. Although this was consistent with the generally accepted notion of competitive ability as a species characteristic (Gaudet and Keddy 1988; Grime et al. 1988; Grace 1990; Goldberg 1996), this result could also be due to the fact that the experiments included only two provenances per species. As much as possible, the provenances were spread over the ranges of the species (Table 5.2), and although not significant, the p-values indicated slight effects. Therefore, differences within the individual species might exist, e.g. in the form of ecotypes, and further studies with a wider range of provenances would be needed to clarify this.

5.7.6 Shoot versus Root Competition

The correlations between the competitive response ranking for shoot competition and those for root competition were not significant, highlighting that shoot and root competition represent two independent mechanisms (Casper and Jackson 1997), and that both need to be considered if we want to fully understand the impact of competition on plants.

Although a direct comparison of the competitive response values for root and shoot competition was not possible, as the experiments were conducted independently, root competition clearly appeared to have the stronger effect on the seedlings. Root competition, therefore, seemed more likely than shoot competition to present an actual threat to the persistence of the *Carmichaelia* species. The significance of root versus shoot competition in their impact on plants has been debated (Keddy 2001). However, the dominance of root competition observed here, was consistent with findings of other competition studies comparing the two mechanisms (e.g., Wilson 1988; Belcher et al. 1995; Gerry and Wilson 1995; Wilson and Tilman 1995; Kosola and Gross 1999).

5.7.7 Implications for Conservation Management

The results illustrated that competition with introduced plants is a dynamic factor whose effect on indigenous taxa varies, depending on the characteristics of the species affected. In particular, it became clear that the relative vulnerability of indigenous plant species to competition correlated with their habitat ecology.

The relationship between tolerance to competition and the habitat ecology of species has been described before. Studies in forest dynamics, for example, have shown that the tolerance of species to light competition is related to their successional status, i.e. to the forest types and successional communities in which they occur (Bazzaz and Wayne 1994; Kobe et al. 1995; Pacala et al. 1996). Catovsky and Bazzaz (2002) found a correlation between habitat preferences of species and their response to nitrogen availability in the soil, which is likely to relate to their response to root competition. The results presented here, showed that these relationships are also relevant in the competition of indigenous species with introduced plants. Knowledge of the habitat ecology of threatened plant species, therefore, could provide a useful tool for the conservation management of these species by allowing predictions on their relative vulnerability to competition. In particular, by distinguishing between above and below ground competition, predictions become possible, stating which species are likely to be the most vulnerable to which component of competition. This would facilitate the setting of priorities in threatened species management.

Among the *Carmichaelia* species, the performance of the two scrub and shrubland species, *C. muritai* and *C. stevensonii,* agreed most strongly with the correlation between habitat characteristics and competitive ability. These species were relatively shade tolerant, being adapted to regeneration in the shady conditions of dense scrub communities, but proved highly vulnerable to root competition, in adaptation to the generally low levels of this

component of competition in their habitats. The conservation management of *C. muritai* and *C. stevensonii* needs to aim at preserving, or restoring, such dense scrub habitats, limiting the invasion of herbaceous plants into the ground layer, as this appeared to pose the most serious threat. Several of the other *Carmichaelia* species, in contrast, were relatively vulnerable to light competition, in particular, the colonisers *C. juncea* and *C. curta*. Their habitats would need to be maintained open to prevent the establishment of taller growing plants competing for light resources with the *Carmichaelia* seedlings.

The climber *C. kirkii* held an outsider position among the *Carmichaelia* species. As expected from its typical scrub habitat, this species showed high tolerance to light competition, but was also relatively tolerant to root competition. This indicated that, similar to other climbing plants (Baars and Kelly 1996), *C.* kirkii is a species of scrub edge habitat rather than the interior. As such, it seemed adapted to the higher levels of invasion by herbaceous plants from adjacent vegetation, characteristic for edge habitats. For the conservation management of *C. kirkii*, its relative tolerance to competition implied that the threat imposed by introduced plants is not as immediate as it is for the other scrub and shrubland species. However, the absolute levels of tolerance would need to be assessed in the field, and unless this is done, conservation management should still aim at limiting invasion of adventives into *C. kirkii* habitats.

The relationship between habitat ecology and vulnerability to competition, shown for the *Carmichaelia* species, is likely to also apply to other threatened plant species. In New Zealand, competition with invading herbaceous plants has been proposed as threat to a number of shrubs typical for dense scrub habitat (e.g., Clarkson and Clarkson 1993; Molloy et al. 1999a), and the results suggest indeed a high vulnerability of such species to this impact. Similarly, several other shrub species that have been described as pioneers of open ground (de Lange and Silbery 1993; Rogers 1996; Shaw and Burns 1997; Widyatmoko and Norton 1997) are likely to face the same threats as *C. curta* and *C. juncea*.

Inferences on the vulnerability of species to competition have to be based on a thorough understanding of the species' habitat ecology. In particular, we need to know which habitat types provide suitable conditions for the regeneration of species, and therefore, support self-sustaining populations. This consideration gains special importance in areas, such as New Zealand, where the natural environment has been severely modified by direct and indirect anthropogenic impacts in recent times. The current habitats of most indigenous species do not represent the original ones in which the species evolved (Wardle 1991). Therefore, we have to clarify whether the current habitats provide suitable conditions for the regeneration of species, before any inferences can be drawn. Chapter 4 illustrated a high degree of

modification for most *Carmichaelia* habitats, but nevertheless, regeneration was found for all species, indicating adaptation to the competitive conditions in the current habitats.

The severe effect of root competition on all the *Carmichaelia* seedlings suggested that especially this component of competition is likely to pose a serious threat to indigenous plant species over a wide range of habitat types. Priority in conservation management and research, therefore, should be given to the control of this impact. The results of the experiments did not allow drawing direct inferences on the performance of the *Carmichaelia* species in their natural habitats. Levels of competition and the precise effects on plants would need to be tested in-situ, preferably by using a research by management approach.

Finally, the results of the study indicated that competition with introduced plants is not the only factor leading to the decline of species. The two common species, *C. australis* and *C. petriei* were surprisingly vulnerable to the impact of shoot, as well as root competition. This suggested that the rarity of the other species is influenced by factors other than competition with introduced plants. Herbivory by introduced mammals (see chapter 6), and other direct and indirect impacts of human land use are likely to also play a role (Mc Clintock 1987). If the conservation of the threatened *Carmichaelia,* and other indigenous plant species is to be successful, all these factors contributing to the rarity and decline of species need to be identified and appropriately addressed in their management.

6 The Impact of Herbivory by Introduced Mammals

6.1 Introduction

This chapter investigates the effect of herbivory by introduced mammals on three species of New Zealand broom, *Carmichaelia*, with the aim of contributing to a better understanding of the significance of herbivory as a threat to rare indigenous plants in New Zealand.

Herbivory by introduced mammals is believed to be one of the main threats to the indigenous New Zealand flora (Wilson and Given 1989; de Lange 1991; Norton 1991; Dopson et al. 1999; Nugent et al. 2001). Although herbivory has always been part of the natural systems, the assemblage of herbivores has changed dramatically since the arrival of humans. Originally, the dominant herbivores were birds and insects (Clout and Hay 1989; Wardle 1991; Table 6.1). In particular, the various species of moa (Dinornithiformes) are thought to have had a major impact on the native vegetation (Wardle 1985; Caughley 1989; Gill and Martinson 1991). Since the arrival of humans, the direct and indirect effects of colonisation have led to the decline or extinction of many of the native herbivore species (Holdaway 1989; Gill and Martinson 1991).

Table 6.1: Native, terrestrial, herbivorous birds of mainland New Zealand and their current status in the wild (Fructivores are excluded; after Moon and Lockley 1982; Gill and Martinson 1991)

Species	**Current Status**
11 species of Moa (Dinornithiformes)	Extinct
Adzebill (*Aptornis otidiformis*)	Extinct
New Zealand geese (*Cnemiornis* sp.)	Extinct
Finsch's duck (*Euryanas finschi*)	Extinct
Paradise duck (*Tadorna variegata*)	Not threatened
Takahe (*Porphyrio mantelli*)	Nationally critical
Kakapo (*Strigops habroptilus*)	Nationally critical
Red / Yellow crowned parakeet (*Cyanoramphus* spp.)	Not threatened/Gradual decline
Kea (*Nestor notabilis*)	Nationally endangered
Kaka (*Nestor meridionalis*)	Nationally endangered
Kokako (*Callaeas cinerea*)	Nationally endangered
Kereru (*Hemiphaga novaeseelandiae*)	Gradual decline

Concurrent with the decline of the native birds, new herbivores were introduced into the country, most of them mammals. The first to arrive was the omnivorous kiore (*Rattus exulans*), which came with Polynesian voyagers possibly as much as 2000 years ago (Holdaway 1999). The main wave of introductions began with the arrival of the Europeans in 1769 (King 1990). Since then, thirty-nine species of herbivorous mammals have been introduced (King 1990), most of them deliberately, as farm and game animals, or for fur production. Others arrived accidentally as stowaways in ships. Twenty-seven of the introduced mammalian herbivores established successfully, with populations known to persist in the wild today (King 1990). Nine of these have become so widespread that they constitute significant components of the New Zealand fauna today (Table 6.2).

The impacts of herbivorous birds on plants differ from the damage caused by mammals (Atkinson and Greenwood 1989). Birds 'pluck and tug', whereas mammals 'cut and manipulate' their food (Lee 2001). In addition, birds are thought to locate their food mainly visually, whereas mammals rely more on their senses of smell and taste (Arnold 1964; Arnold et al. 1980; Atkinson and Greenwood 1989). The divaricate growth form, typical of a range of New Zealand shrubs and juvenile trees, is thought to be an adaptation to bird herbivory (Greenwood and Atkinson 1977; Mc Queen 2000). Other possibly adaptive characteristics include prostrate growth form, mimicry and reduced visual apparency (Atkinson and Greenwood 1989). However, as these traits evolved under the selective pressure of browse by birds, they do not necessarily provide the same degree of protection from browse by mammals.

Table 6.2: Introduced, terrestrial, herbivorous mammals of mainland New Zealand, time of introduction, and their current status in the wild (Fructivores are excluded; after King 1990; Atkinson 2001).

Species	**Time of Introduction**	**Current Status**
Brushtail possum (*Trichosurus vulpecula*)	1858-1940	Widespread
European rabbit (*Oryctolagus cuniculus*)	1777-1860s	Widespread
Brown hare (*Lepus europaeus occidentalis*)	1863-1875	Widespread
Pig (*Sus scrofa*)	1773-1790s	Widespread
Chamois (*Rupicapra rupicapra*)	1907, 1914	Widespread
Goat (*Capra hircus*)	1773, 1777	Widespread
Red deer (*Cervus elaphus scoticus*)	1851-c. 1919	Widespread
Ship rat (*Rattus rattus*)	c. 1860-1870 (Nth Island) c. 1885-1895 (Sth Island)	Widespread
House mouse (*Mus musculus*)	c. 1830 (Nth Island) 1850s (Sth Island)	Widespread
19 further species of mammals	since 1769 (2000 BP for kiore)	Localised or rare

Soon after the introduction of the mammalian herbivores into New Zealand, changes in the native vegetation were observed (e.g., Moore and Cranwell 1934; Holloway 1950; Poole 1951), and today, numerous studies illustrate how introduced herbivores modify the structure and composition of native vegetation (e.g., James and Wallis 1969; Veblen and Stewart 1980; Allen et al. 1984; Stewart et al. 1987; Rose and Platt 1987, 1992; Campbell 1990; Rogers 1991; Nugent et al. 2001). A frequently observed pattern is that palatable species decrease in abundance while non-palatable species increase (Allen et al. 1984; Mark 1989; Smale et al. 1995; Fitzgerald and Gibb 2001). However, as most of the studies focus on vegetation and plant communities, they provide little information on the significance of these changes for individual species and the actual processes involved.

In general, browse can negatively affect the dynamics of a plant population in two ways: through an increase in plant mortality or a decrease in seed production (Crawley 1983; Watkinson 1986; Hendrix 1988). An increase in mortality will lead to a decline in the plant population, if the browse-inflicted mortality exceeds the level that would be reached in any case, through the influence of other factors. Similarly, reduced seed production will lead to a population decline, if it reaches a level at which regeneration within the population becomes actually limited by the availability of seeds (Crawley 1983; Watkinson 1986; Hendrix 1988).

These impact-effect relationships have only been studied for very few plant-herbivore systems in New Zealand. Most attention has probably been paid to the effect of possums on forest trees and shrubs. Here, severe browse has been shown to increase plant mortality and to consequently lead to a decline of favoured food species in the forest (Meads 1976; Leutert 1988; Pekelharing et al. 1998a, b; Payton 2000). Increased mortality has also been found for the shrub *Muehlenbeckia astonii,* as a consequence of sheep and lagomorph browse (de Lange and Silbery 1993; Norton 2001). Reductions in seed production have been observed for nikau (*Rhopalostylis sapida*) and hinau (*Elaeocarpus dentatus*) as a result of possum browse (Cowan and Waddington 1990; Cowan 1991), and for *Anisotome haastii*, when browsed by goats (Norton 1995b). Possums and kiore target the flowers of *Dactylanthus taylorii*, a rare perennial holo-parasite, and completely prevent seed production, while ship rats act as effective pollinators on these plants (Ecroyd 1996).

6.2 Objective and Research Approach

The objective of this study was to clarify the significance of herbivory by introduced mammals as a threat to the genus of the native New Zealand broom, *Carmichaelia*. As nitrogen fixing plants these species are likely to be particularly attractive to mammalian herbivores (Crawley 1983; Ritchie et al. 1998). Accordingly, severe browse has been observed on most species within the genus (Purdie 1985; Heenan 1995; Priantoro 1995; Heenan 1996b; Norton et al. 1998; Dopson et al. 1999; Heenan and de Lange 1999; Molloy et al. 1999b; Wardle 2000a, b; and pers. obs.). In addition, diet studies on a number of introduced mammals have found *Carmichaelia* as part of their food resource (Hughes 1975; Asher 1979; Blay 1989; Cochrane 1994; Parkes and Thomson 1995; Reddiex 1998; Yockney and Hickling 2000). Despite these numerous observations, however, it is unclear whether herbivory by introduced mammals poses an actual threat to the persistence of *Carmichaelia* species, as the precise effects on plants and the consequences for the persistence of populations have not been investigated.

Three species of *Carmichaelia* at four different sites were included in the study to allow for comparison and thus, gain insight into factors influencing the significance of herbivory as a threat. Two of the species, *Carmichaelia juncea* and *C. hollowayi*, are currently listed as 'Nationally Endangered' and 'Nationally Critical', respectively (de Lange et al. 1999), surviving only in a few isolated populations. The third species, C*. vexillata,* is considered to be in 'Serious Decline' (de Lange et al. 1999). For all three species, herbivory by introduced mammals has been suggested as a major threat to their persistence (Wilson and Given 1989; Norton et al. 1998; Molloy et al. 1999b; Wardle 2000b). As they are low growing dwarf shrubs they seem likely to be subject to browse and grazing by most introduced mammalian herbivores.

Using exclosure trials, I compared the performance of plants that were protected by cages with the performance of unprotected plants. The focus was on the effects of herbivory on plant mortality and seed production, and the resulting consequences for the population dynamics of the species.

6.3 Methods

The exclosure trials were set up in populations where browse by introduced mammals had previously been observed. I chose two locations for *Carmichaelia juncea*, and one each for *C. vexillata* and *C. hollowayi* (Table 6.3). The following two sections outline the general methodology, then further details and variations for the individual sites are described.

Table 6.3: Locations and experimental design of the exclosure trials (for details see text).

Species	Location	Treatments	Replication	Branches per plot
C. juncea	Waiho River, Franz-Josef, South Westland, islands in riverbed	Caged / uncaged plants	5	12
C. juncea	Welcome Flat, Copland Valley, South Westland, river flats	Caged / uncaged plants	3	12
C. vexillata	Pukaki-Ohau Canal, Mackenzie Basin, sidewall of hydro-canal	Caged / uncaged plants	10 (5)	6
C. hollowayi	Awahokomo limestone, Waitaki Valley, top of limestone outcrop and colluvium	Caged plants / uncaged plants (without stock access) / uncaged plants (with stock access)	10	6

6.3.1 Experimental Design

The exclosures were built as cages with 90x90x45 cm frames made of wood or metal covered by wire netting (Fig. 6.1A). The 30 mm mesh used for *C. juncea* in the Waiho River, protected the plants from all herbivores larger than rats. At the other sites, I used 12 mm mesh, which excluded all animals larger than mice. The uncaged plants remained accessible to all herbivores present at a site.

At each site several pairs of neighbouring plants were chosen as replicates, and the plants of each pair were randomly assigned to either the cage or the uncaged treatment. All plants selected within one population were comparable in size and apparent state of health, and all plants showed signs of previous browse, except for some *C. juncea* in the Waiho River. On each plant several branches were marked with numbered metal tags tied around the base of

a stem, close to the ground, and a green twist tie around a node further up. The latter formed the base mark for the assessments (Fig. 6.1B).

A

B

Fig. 6.1: A - Exclosure for *C. juncea* in the Waiho River. The cage is built with a wooden frame and wire mesh. B - Tags on a branch of *C. juncea*. The metal tag at the base of the stem shows the branch number. The green twist tie marks the node from which measurements and counts started.

The trials were established in December 1999 and subsequently visited at 1-7 month intervals until November 2001 (Table 6.4).

Table 6.4: Timing of visits to the four exclosure trials (for details see text).

	***C. juncea*, Waiho River**	***C. juncea*, Welcome Flat**	***C. vexillata***	***C. hollowayi***
Dec 99	√	√	√	(√)
Jan 00	√	√	√	(√)
Feb 00	√	√	√	(√)
Mar 00	√	√	√	√
Apr 00	√	√	√	√
May 00		√	√	√
July 00	√			
Oct 00			√	√
Nov 00	√	√	√	√
Jan 01			√	√
Feb 01				√
Mar 01			√	√
Apr 01	√	√	√	
Nov 01	√	√	√	√

6.3.2 Data Collection

The efficacy of the treatments, i.e. the timing and intensity of browse affecting the unprotected plants during the trial period was assessed by measuring the cumulative length of the tagged branches at each visit (Table 6.5). Cumulative length was defined as the length of the tagged main shoot plus the lengths of all its side shoots above the base mark. Only live tissue was included. If a branch had been browsed or died back below the base mark, a new branch was randomly chosen, marked, and measured, to keep the total number of branches per plot constant. These measurements reflected tissue loss and gain of the plants during the trial period. The herbivores present at a site were identified by their distinctive browse marks on the plants and animal sign in the surrounding area (prints and faeces).

The effects of herbivory on the plants and their populations were assessed by recording plant mortality and seed production. Mortality was recorded for the plants as a whole, while seed production was assessed using the tagged branches. At each visit, the numbers of buds, flowers, immature pods, and mature pods on the branches were counted. Inferences on the consequences of plant mortality for the plant populations were drawn from the comparison of caged and uncaged plants. The incidence of seed limitation of regeneration due to reduced seed production was assessed by monitoring recruitment in the plots. At the beginning and the end of the trial period, seedlings were counted inside the cages and in an equivalent area around the uncaged plants. Where a reduction in seed production on the unprotected plants was observed during the monitoring (only *C. juncea*, Waiho River), recruitment was also assessed at the end of both summers.

Table 6.5: Assessments performed during the monitoring period.

Assessment	**Measurement / Count**	**Frequency**
Timing and intensity of browse	Cumulative lengths of branches	Each visit
Herbivores present	Browse marks on plants, animal sign in the area	Each visit
Effect on plant mortality	Plant death	Each visit
Effect on seed production	Flower and pod numbers on branches	Each visit
Seed limitation of regeneration	Numbers of seedlings in plots	First and last visit (+ end of both summers for *C. juncea*, Waiho River)

6.3.3 *C. juncea*, Waiho River

In the Waiho River, *C. juncea* occurs on relatively young and unstable surfaces in a dynamic braided riverbed. Five replicates were established in an area of the riverbed that was at the time thought to support the main population (Table 6.3). Since then the known population has been extended for several km downstream. Prior to the start of the trial, several of the known 'sub-populations' on different islands in the riverbed had been swept away during a flood. To reduce the risk of losing plots during the trial, it was decided to spread the replicates over several islands. All plots were established on the true right of the riverbed to allow all-weather access. After an extensive search, four islands with sufficient plants for five replicates were found, spread over a distance of c. 1 km. Each plot comprised two plants, and six branches were tagged on each of these, enabling 12 branches per plot to be assessed. The branches were primary stems originating from a central rootstock, and the base marks for the assessments were located close to the base of the stems. The number of branches per plot varied for the uncaged plants throughout the trial, as the browse damage was at times so severe that no branches remained to which new tags could be tied.

6.3.4 *C. juncea*, Welcome Flat

At Welcome Flat, *C. juncea* occurs on older, relatively stable surfaces on the main river flats and low terraces. The initial design of the trial was identical to that in the Waiho River. Replication was restricted more by logistical constraints, as it was very expensive to fly the material for the cages into the valley (18 km from nearest road). The five replicates were spread over three different areas of river flat, on a 2 km stretch of the Copland River. During the trial, two of the caged plants and two of the uncaged plants were identified as hybrids with *C. arborea*, thus, reducing replication for true *C. juncea* to three. As in the Waiho River, 12 branches were assessed per plot, but they were mostly higher order shoots towards the end of the main stems. This was necessary to minimise disturbance during the assessments, as the branches grew through the dense vegetation associated with this site (see section 4.4.1.2).

Department of Conservation staff assisted with the assessments of both *C. juncea* trials. Measurements were made monthly during the first summer and at less frequent intervals during summer 2000/2001 (Table 6.4).

6.3.5 *C. vexillata,* Pukaki-Ohau Canal

The trial site for *C. vexillata* was located along the side wall of the Pukaki-Ohau Canal (Fig. 6.2). The present population of *C. vexillata* must have established since the construction of the hydro-canals in the late 1970s. Ten replicates were established in the first season. In the second summer, five of the caged plants were used as part of a different study, reducing the number of caged plants (and true replicates) to five. On each plant 6 branches were measured. Due to the growth habit of this species they were of secondary or higher order.

Fig. 6.2: Exclosure trial for *C. vexillata* along the Pukaki-Ohau Canal, Mackenzie District. The plants are located alongside the slope flanking the canal.

During the first summer, it became clear that the assessment of reproductive activity with flower and pod counts on individual branches was not a suitable method for *C. vexillata*. The branches tagged on this species were very short and produced only one to three flowers each. However, as an average sized plant consisted of several hundreds of branches, the overall number of flowers and pods per plant was sometimes very high depending on how many branches were involved in flowering. The low numbers counted for the individual branches, therefore, did not reflect the actual reproductive activity of the plants. In summer 2000/01, a ‘flower and pod score’, which assessed the number of flowers and pods for the whole plants, was introduced. The score categories used were:

0 - no flowers/pods present,
1 - sparse, < 20 flowers/pods on plant,
2 - scattered, 20 - 100 flowers/pods on plant,
3 - medium, > 100 flowers/pods on plant, up to half of the branches involved,
4 - heavy, > 100 flowers/pods on plant, over half of the branches involved.

6.3.6 *C. hollowayi,* Awahokomo

At Awahokomo, *C. hollowayi* occurs on a limestone outcrop located within grazed farmland. The plants grow on top of the outcrop as well as on the colluvial slopes around it. One part of the outcrop is inaccessible to sheep, but rabbits, possums, and rats have been observed there (Molloy et al. 1999b). Three treatments were established (Table 6.3). Ten exclosure plots and paired unprotected plants were selected on top of the rock outcrop where sheep had no access (Fig. 6.3). A further ten plants were selected on the colluvial slopes for the treatment ‘uncaged (with sheep access)’. On each plant six branches of secondary or higher order were tagged for the assessments. Due to initial difficulties with the marking of the branches, the measurements of the branch lengths did not begin until March 2000 (Table 6.4).

Fig. 6.3: Exclosure trial for *C. hollowayi* at Awahokomo, Waitaki Valley.

6.3.7 Analysis

A prerequisite for the validity of the trials is that there were no significant differences between the treatments regarding the characteristics of the tagged branches. I analysed this using paired comparison for *C. vexillata* and the plants of *C. hollowayi* located on top of the rock outcrop ('caged' and 'uncaged (without sheep access)'). The latter were compared in t-tests with the uncaged plants on the colluvial slopes (with stock access). In the two *C. juncea* trials replication was too low to allow meaningful tests, and I assumed non-significant differences by simply comparing the means of the two treatments.

To illustrate the timing and intensity of browse at the trial sites the initial branch lengths were set as zero. The losses (or gains) per branch from one visit to the next were calculated, and added cumulatively over the monitoring period. I chose this procedure over the use of the absolute branch lengths, because the assessments did not always follow the same tagged branches throughout the monitoring period, as dead branches or branches browsed below the base mark were replaced. The resulting cumulative tissue loss (or gain) was used as a descriptive measure for the browse intensity at the sites. It did not measure the overall growth or tissue loss of the plants.

Mortality, seed production, and regeneration were compared between the treatments to identify the effects of herbivory on these variables. Detailed statistical analyses were not performed due to the small samples sizes. Variability of the data was expressed as standard error (SE) of the calculated means.

6.4 Results

Table 6.6 summarises the observed browse intensities and the effects on the uncaged plants at the four study sites. The browse intensity varied considerably between the sites. Effects on plant mortality were not observed, and effects on seed production and regeneration only for *C. juncea* in the Waiho River.

Table 6.6: Browse intensity and effects on the uncaged plants in the four trials.

Trial	Browse intensity	Mortality	Seed production	Regeneration
C. juncea, Waiho River	High	No effect	Reduced	Reduced
C. juncea, Welcome Flat	Nil	No effect	No effect	No effect
C. vexillata	Fluctuating	No effect	No effect	No effect
C. hollowayi	Nil to low	No effect	No effect	No effect

6.4.1 *Carmichaelia juncea*, Waiho River

6.4.1.1 Browse Intensity

The browse intensity on the uncaged plants of *C. juncea* in the Waiho River was very high throughout the monitoring period (Fig. 6.4). Initially, the branches of the trial plants were of similar lengths (31 ± 3.0 cm on the caged plants and 34 ± 6.4 cm on the uncaged plants). In the three weeks following trial establishment, the uncaged plants suffered severe browse reducing the branch lengths to only a few cm. They then re-sprouted with side shoots, but any fresh growth was continually browsed off, turning the plants into stumps with clusters of short branches (Fig. 6.5a). In contrast, each branch of the caged plants gained an average of 21 metres in cumulative length, resulting in dense mats of entangled branches inside the exclosures by November 2001 (Fig. 6.5b). The branch tips on the uncaged plants were cut at the 45°-angle typical for browse by hares (Wong and Hickling 1999), and hare droppings were found abundantly around the plants (Fig. 6.6). No other animal sign was observed.

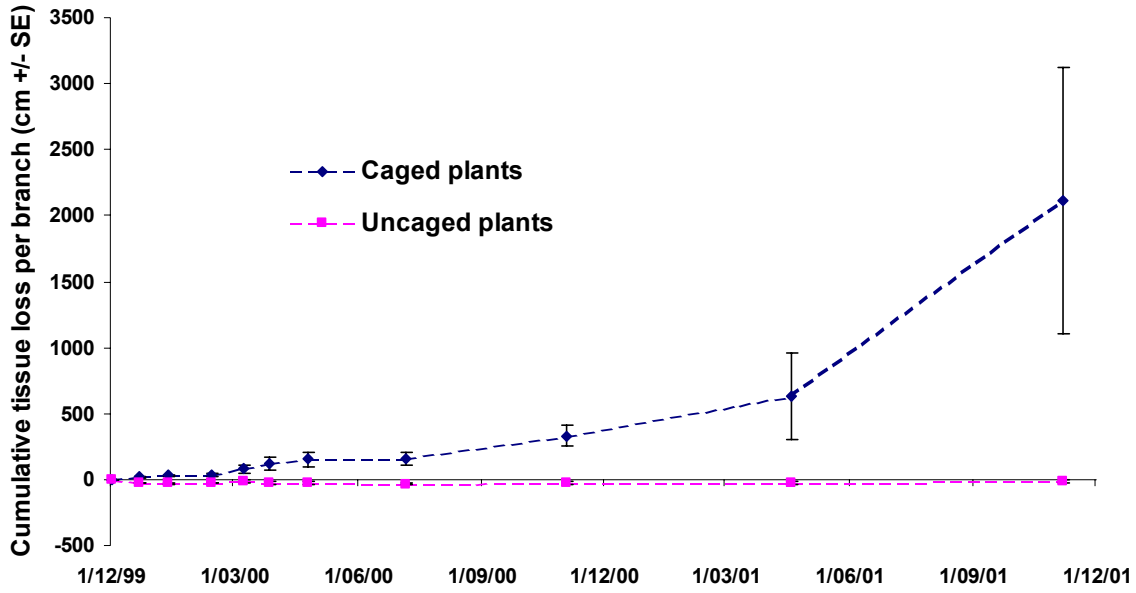


Fig. 6.4: Tissue loss (and gain) of branches of caged and uncaged plants of *C. juncea*, Waiho River, Franz-Josef.

A

B

Fig. 6.5: Uncaged (A) and caged (B) plants of *C. juncea* at the beginning of the trial (left) and after 2 years (right). Continual browse reduced the uncaged plants to stumps with clusters of short side branches. The caged plants grew vigorously forming a dense mat of branches inside the exclosures.

Fig. 6.6: Freshly browsed plant of *C. juncea*, Waiho River. The traces of the removed branches are visible in the sand. Hare droppings are scattered around the plant.

6.4.1.2 Mortality and Seed Production

The browse damage had no immediate impact on plant mortality, as no plants died during the monitoring period. The effect on seed production, however, was very pronounced (Fig. 6.7). At the start of the trial, the branches of both, caged and uncaged plants carried approximately 60 flowers each and a few immature pods. During the following months, the caged plants produced more flowers and pods. This reproductive activity was strongly inhibited on the uncaged plants. Only a few flowers were found at the second visit, and no mature pods were produced on the plants. The same pattern was observed during summer 2000/01, with the caged plants flowering and seeding abundantly and the uncaged plants producing a few flowers but no pods (V. Harrison, DoC Franz-Josef, pers. comm.).

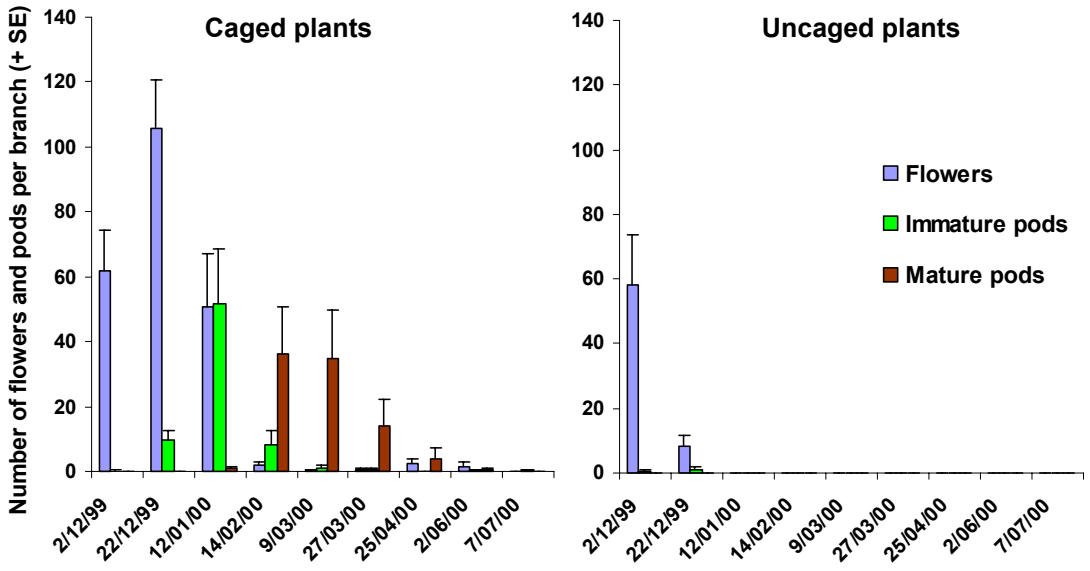


Fig. 6.7: Reproductive activity of caged and uncaged plants of *C. juncea*, Waiho River, Franz-Josef, during summer 1999/2000.

6.4.1.3 Regeneration

The pattern of regeneration in the plots also showed obvious differences between the two treatments (Fig. 6.8). At the start of the trial, in December 1999, no seedlings were found around any of the trial plants, although some were present next to plants nearby. During the two years of monitoring, *C. juncea* seedlings were found in all five exclosure plots, but only in one of the uncaged plots. After various flood events, three of each, caged and uncaged plots, remained at the final measurement. All cages had abundant seedlings in them (350 - c. 2000 seedlings per plot), while only one of the uncaged plots contained a single seedling.

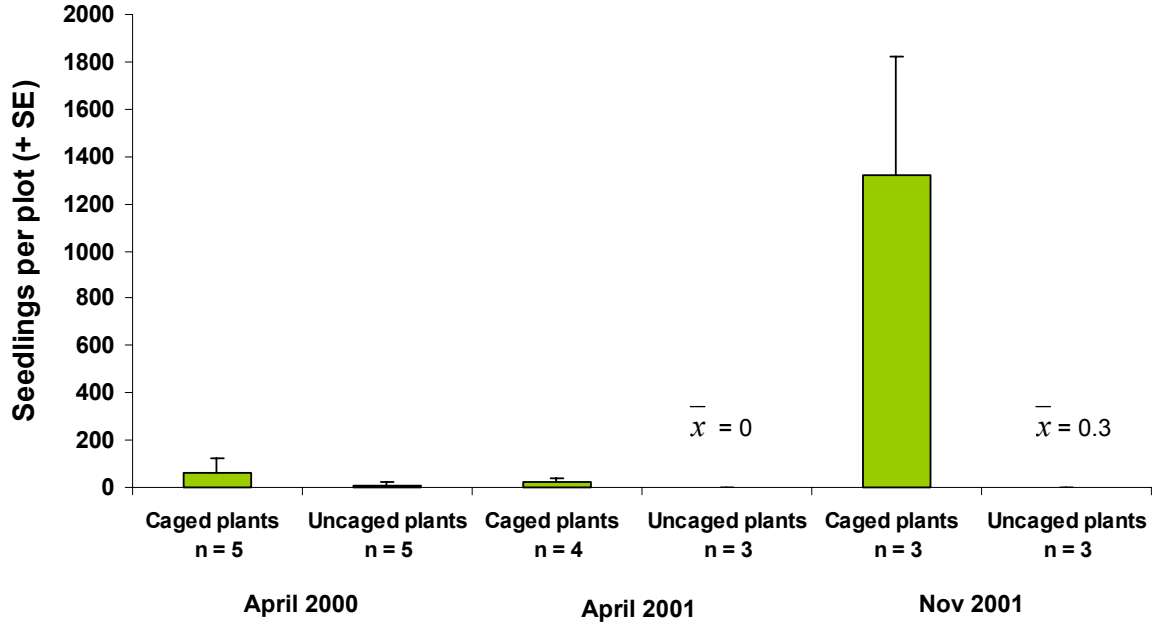


Fig. 6.8: *C. juncea* seedling numbers in caged and uncaged plots, Waiho River, Franz-Josef.

6.4.2 *Carmichaelia juncea*, Welcome Flat

6.4.2.1 Browse Intensity

At Welcome Flat, no fresh browse was observed on *C. juncea*, although possum and chamois droppings were found in the area. The tagged branches were initially about 15 cm long (caged plants: 14 ± 1.2 cm; uncaged plants: 16 ± 4.0 cm). During the monitoring period, the total loss in cumulative length per branch added up to almost 40 cm for the uncaged plants (Fig. 6.9). (The total can exceed the initial length, as dead branches were replaced throughout the trial.) The reason for the die-back could not be identified, but did not appear to be related to the treatments, as the branches of the caged plants also lost in length, although not quite as pronounced. The branches showed no obvious signs of browse damage, but simply died back from the branch tips. At the last visit, in November 2001, all plants had died back severely, but most of them re-sprouted with new shoots from the base.

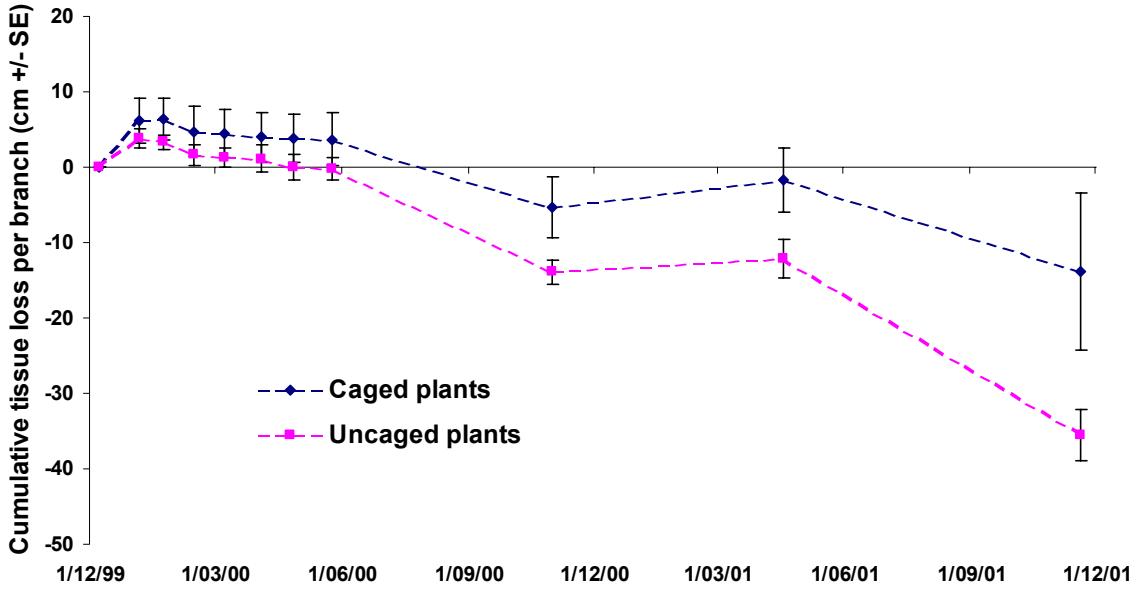


Fig. 6.9: Tissue loss (and gain) of branches of caged and uncaged plants of *C. juncea* at Welcome Flat, Copland Valley.

6.4.2.2 Mortality and Seed Production

Differences between the treatments regarding plant mortality and seed production were not observed. Despite the dramatic loss of branches, none of the plants actually died completely. At the start of the trial, the branches of both groups of plants carried about 35 flowers each, and fully completed the generative cycle during the summer (Fig. 6.10).

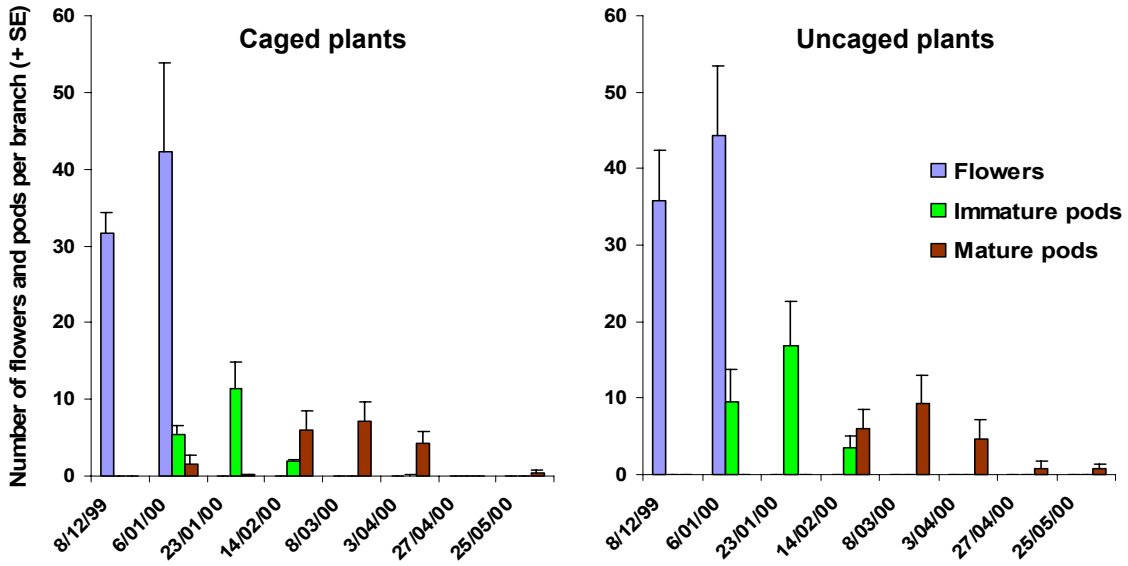


Fig. 6.10: Reproductive activity of caged and uncaged plants of *C. juncea*, Welcome Flat, Copland Valley, during summer 1999/2000.

6.4.2.3 Regeneration

Differences in *C. juncea* seedling numbers between the treatments were also not apparent (Fig. 6.11). No seedlings were observed in any of the plots in December 1999. In November 2001, recruitment was prolific, with seedling numbers ranging from 125 to 2000 per plot in both treatments. An exception was one uncaged plot that had recently been flooded, and did not show regeneration. Most seedlings were only about 1 cm tall, suggesting they had emerged after the winter.

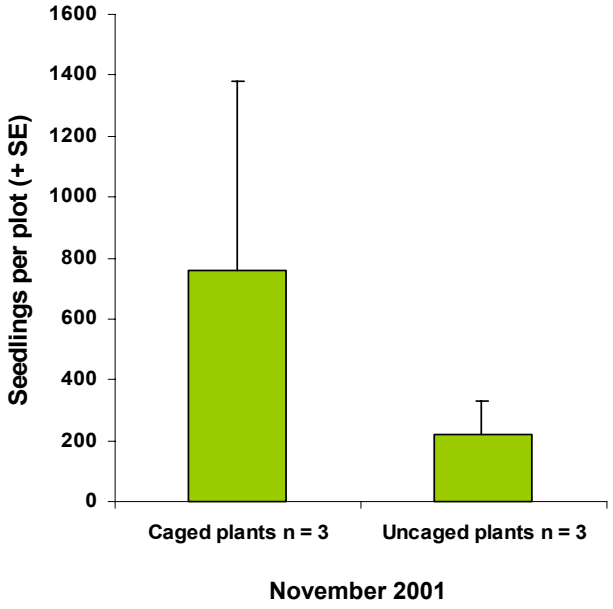


Fig. 6.11: *C. juncea* seedling numbers in caged and uncaged plots, Welcome Flat.

6.4.3 *Carmichaelia vexillata*

6.4.3.1 Browse Intensity

The browse intensity on *C. vexillata* at the Pukaki-Ohau Canal fluctuated during the monitoring period (Fig. 6.12). Initially, there was no difference in branch length between caged and uncaged plants ($p = 0.317$; mean length: 4.8 ± 0.1 cm). During summer 1999/2000, only occasional browse was observed, causing little change in branch lengths. During winter, however, the branches of the uncaged plants were browsed back to stumps of about 2 cm in length (Fig. 6.13). During summer 2000/01, the browsing pressure was again low, allowing some of the branches to recover. Both, caged and uncaged plants, grew by forming side shoots on the tagged branches. This new growth was again browsed on the uncaged plants during winter 2001. The browse marks on the plants were typical of hare (Wong and Hickling 1999; Fig. 6.13), and hare droppings were abundant around the plants. No other animal sign was observed.

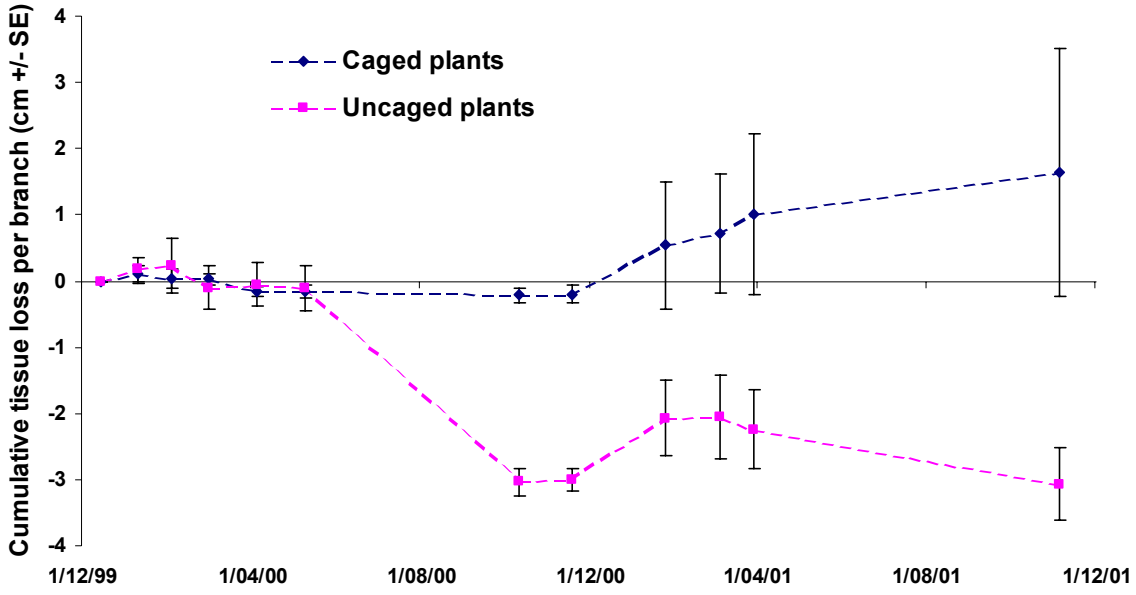


Fig. 6.12: Tissue loss (and gain) of branches of caged and uncaged plants of *C. vexillata*, Pukaki-Ohau Canal.

6.4.3.2 Mortality and Seed Production

The browse damage had no effect on plant mortality or seed production. None of the plants died during the trial period. During summer 1999/2000, all plants flowered and fruited abundantly. In the second summer the flowering activity appeared reduced, but differences between the two treatments were not observed (Fig. 6.14). Large numbers of flowers and pods were present on both, caged and uncaged plants.

Fig. 6.13: Uncaged plant of *C. vexillata*, Pukaki-Ohau Canal, after the browse event during winter 2000. The browse marks were typical of hare impact.

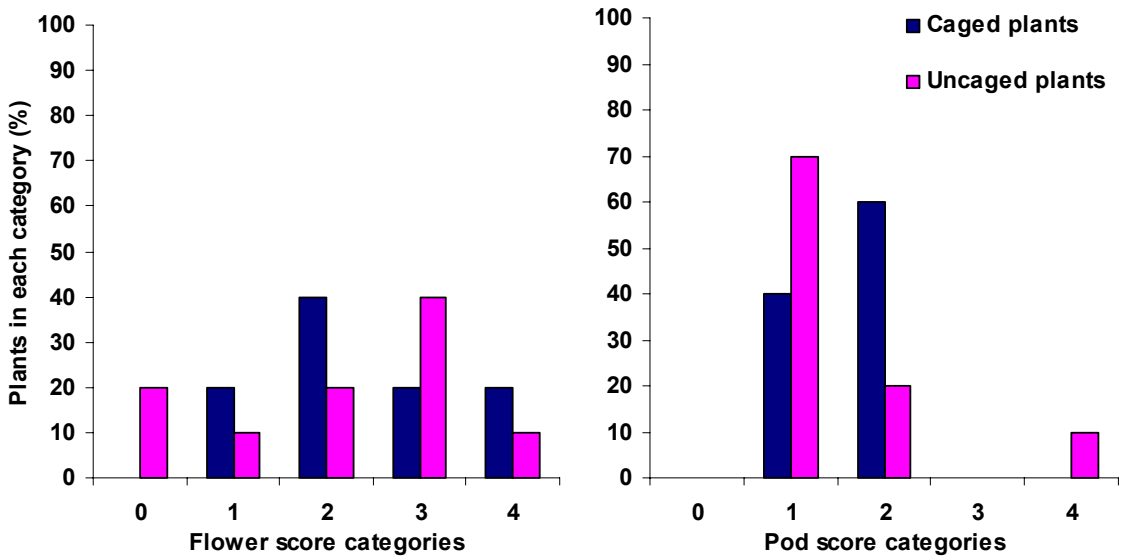


Fig. 6.14: Abundance of flowers and pods on *C. vexillata* during summer 2000/2001. Plants were categorised according to their maximum score during summer (0 - no flowers/pods, 1 - < 20 flowers/pods, 2 - 20 - 100 flowers/pods, 3 - > 100 flowers/pods, up to half of the branches involved, 4 - > 100 flowers/pods, over half of the branches involved.)

6.4.3.3 Regeneration

No seedlings were found at this site.

6.4.4 *Carmichaelia hollowayi*

6.4.4.1 Browse Intensity

The browsing pressure on *C. hollowayi* at Awahokomo varied with the accessibility of the plants (Fig. 6.15). The plants on top of the rock outcrop, which were not accessible to sheep, were not browsed during the trial period, despite the fact that rabbit and possum sign was observed. The branches were initially 8.5 ± 0.2 cm long (comparison of caged plants and uncaged plants without sheep access: $p = 0.336$) and changed in length by less than ± 1 cm over the monitoring period. The branches of the uncaged plants on the colluvial slopes, which were accessible to sheep, were initially slightly longer, although differences were not significant ($p > 0.062$), and also more variable (12 ± 1.8 cm). During the first year of the trial, sheep occasionally browsed the accessible plants, but the impact was never severe and no tagged branches were browsed. In the second winter, however, these plants were heavily browsed, with a loss of approximately 3 cm per branch. The frayed branch tips indicated sheep browse.

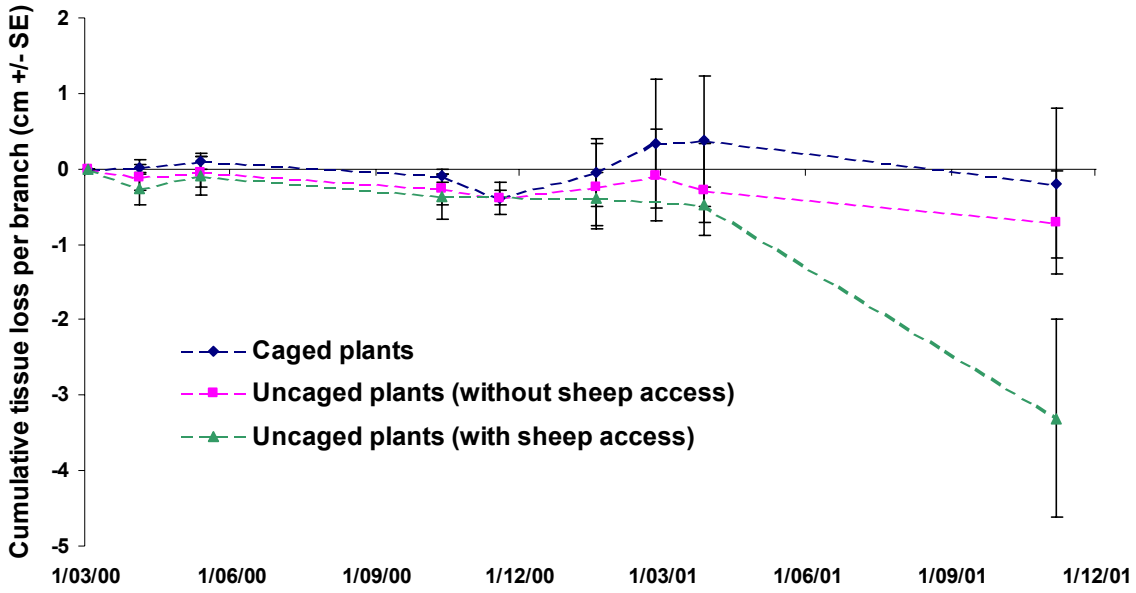


Fig. 6.15: Tissue loss (an gain) of branches of caged and uncaged plants of *C. hollowayi* at Awahokomo, Waitaki Valley.

6.4.4.2 Mortality and Seed Production

No differences were observed between the three groups of plants regarding survival or seed production. None of the plants died, and reproductive activity was very low during both summers. Half of the plants in each treatment did not show any signs of flowering at all. The other plants produced sporadic flowers and pods on very few branches.

6.4.4.3 Regeneration

Due to the suckering growth habit of *C. hollowayi* it was impossible to distinguish true seedlings from rhizomatous young shoots, especially as both appear with juvenile morphology. At the beginning of the trial, one possible seedling, 14.3 cm tall, was found amongst the branches of an adult plant in area accessible to sheep. This seedling was repeatedly browsed, and, although it re-sprouted, reached only 8.5 cm in length in November 2001. Five further possible seedlings were found in cages as well as around uncaged plants at the last visit.

6.5 Discussion

6.5.1 Browse Intensity

The browse intensities at the four study sites varied from nil to high, and from continual to variable over time.

At Welcome Flat, no fresh browse was observed despite the presence of the herbivores chamois and possums. *Carmichaelia* species form a major component of the diet of chamois in Westland (Parkes and Thomson 1995; Yockney and Hickling 2000), and although no possum diet study to date has detected *Carmichaelia* as part of their diet, possum damage has been observed on several species (G. Loh, DoC Dunedin, pers. comm.; pers. obs.). Similarly, at Awahokomo, rabbits and possums did not feed on *C. hollowayi* during the trial period, despite findings that rabbits positively select for *Carmichaelia* species (Reddiex 1998). This suggested that the presence of herbivores does not necessarily imply that plants are actually subject to browse. However, all plants showed signs of previous browse damage, suggesting that herbivory at the sites occurred intermittently. The two year monitoring period may have been too short to capture this.

Low densities in the herbivore populations and sufficiently available alternative food resources might have reduced the impact on the *Carmichaelia* plants during the trial period (Crawley 1983; Illius and O'Connor 2000). The density of the chamois population in the Copland Valley is maintained at moderate levels by commercial and recreational hunting (T. Farrell, DoC Hokitika, pers. comm.). Possum numbers are also likely to have been low, as a control programme was conducted in the area of Welcome Flat in June 2000 (P. van Klink, DoC Haast, pers. comm.). Nothing is known about the possum population at Awahokomo,

but rabbit numbers have drastically declined since the introduction of the RHD virus in1997 (Norbury 2001; E. Matheson, Kurow, pers. comm.).

The increase in sheep impact on the accessible slopes at Awahokomo was probably caused by higher stocking levels during winter 2001. Sheep consume *Carmichaelia* species only as a minor food component without positive selection (Hughes 1975). At the Pukaki-Ohau Canal, the active herbivores were hares, and the observed seasonal fluctuation in browse intensity was consistent with findings by (Blay 1989), who related the increased consumption of *Carmichaelia* by hares during the winter months to seasonal variation in food availability (see also Horne 1979).

Hares were also identified as herbivores on *C. juncea* in the Waiho River. The browsing pressure here was severe throughout the study, possibly reflecting the sparse vegetation cover in the riverbed, which provides limited alternative food resources. Furthermore, the hares seemed to specifically target *C. juncea*, as in one case they climbed through a gap into one of the cages that was temporarily overhanging a steep bank (Fig. 6.16).

Fig. 6.16: One of the cages in the Waiho River after a flood-event. The cage stood out over the edge of a steep bank, and hares climbed through the gap to feed on the *C. juncea* plants (photo: V. Harrison, DoC Franz-Josef).

A limitation to the above is that the assessed browse intensities do not necessarily reflect the actual browsing pressures at the sites, i.e. under 'undisturbed' conditions. The installation of the exclosures, the tagging of branches, and the regular visits might have altered herbivore behaviour and thus, the browsing pressure on the plants (Cahill et al. 2001). However, at least for the Waiho River site, this seemed not to be the case, as severely browsed plants of *C. juncea* had been observed prior to the trial (and had prompted the choice of trial site). During the monitoring period, plants in other areas of the riverbed showed the same level of damage as uncaged plants, and a wider search for seed pods in February 2000, when pods were abundant on caged plants, was unsuccessful.

In the exclosure treatment, the cages themselves are likely to have had an effect on the plants by altering the microclimate and other factors, such as the intensity of invertebrate herbivory or the activity of pollinators (Southwood and Henderson 2000). The fact that the branches of the caged plants at Welcome Flat and Awahokomo performed slightly better, even though no browse was observed on the paired uncaged plants, suggested such an effect. This could potentially have confounded the effects of herbivory on the plants. However, no treatment differences in plant mortality, seed production, and regeneration were found at these two sites, indicating that the cages did not influence these variables.

6.5.2 Effects of Herbivory on Plant Mortality

Herbivory was not found to affect mortality of the three *Carmichaelia* species studied. Even in the Waiho River, where *C. juncea* was subject to continual severe browse damage, none of the plants died. However, with 2 years, the trial period was relatively short, and longer term monitoring could well reveal an effect on plant survival. For the duration of this study, *C. juncea* and also *C. vexillata* showed a strong tolerance to herbivore damage with new growth developing after browse events. This ability to re-sprout after browse damage was also observed for several other *Carmichaelia* species (*C. astonii*, *C. australis*, *C. crassicaule, C. curta*, *C. hollowayi*, *C. kirkii*, *C. petrii* ; pers. obs.), and is characteristic of a number of New Zealand shrub species (e.g., Flux 1967; de Lange and Silbery 1993; Molloy and Clarkson 1996).

The die-back observed on *C. juncea* at Welcome Flat was not related to any herbivore damage. Growing in braided riverbeds and on young river terraces, *C. juncea* is a species of a very dynamic habitat. In adaptation to this it is likely to have fast-growing, short-lived individuals. The caged plants in the Waiho River population demonstrated the remarkable growth rate of this species by gaining over 20 m in cumulative length per branch over the trial

period. The plants at Welcome Flat, in contrast, seemed to represent senescing adults, that died back concurrent with abundant regeneration.

While adult plants are often relatively resistant to herbivore damage, seedlings and juveniles usually represent more sensitive stages (Crawley 1983; Hendrix 1988; Hulme 1996). In New Zealand, this has been observed for the rare shrub *Melicytus drucei* , where hare and possum browse did not kill the adults, but destroyed any regeneration (Molloy and Clarkson 1996). This study focused on the effects of herbivory on adult plants, but to fully understand the impact of herbivores on the persistence of *Carmichaelia* species, the effects of browse on the mortality of seedlings and juveniles need to be investigated.

6.5.3 Effects of Herbivory on Seed Production

The severe browse damage on *C. juncea* in the Waiho River almost completely prevented seed production, while *C. vexillata* did not suffer any obvious reduction in fecundity. It appeared that the architecture of the plants protected the flowers and pods from the browse damage. *C. vexillata* produced flowers over the whole length of the stems, i.e. on young as well as older wood. Many flowers were located close to the ground, jammed in between the densely arranged branches, where they were unlikely to be consumed. *C. juncea* also produced flowers over the whole length of their stems, but, due to the open growth habit of the plants, they seemed to be more vulnerable to browse damage. Correlations between vulnerability to herbivory and plant architecture have also been observed for other species, although the exact details vary with the specific growth form of the plants. Mc Intyre (1996), for example, found that the size and shape of their rosettes influences the vulnerability of Asteraceae to grazing (see also Marquis 1996; Hadar et al. 1999; Stowe et al. 2000).

Another reason for the better performance of *C. vexillata* under the impact of herbivory was probably the difference in the timing of the impact (Crawley 1983; Hendrix 1988; Whigham and Chapa 1999). While *C. juncea* was subject to severe browse throughout the monitoring period, serious damage was restricted to the winter months for *C. vexillata*, allowing the plants to recover and flower during summer. In other populations of *C. vexillata*, where the plants appeared to be subject to more frequent, severe browse, I observed plants that were damaged to a degree that did not allow any reproductive activity.

6.5.4 Consequences for the Persistence of Populations

Herbivory by introduced mammals did not appear to pose a threat to the persistence of the *Carmichaelia* species through an increase in their adult mortality, at least not at the temporal scale considered in this study. However, the strong negative effect on the fecundity of *C. juncea* in the Waiho River, together with the markedly reduced recruitment in the uncaged plots at this site, suggested that the herbivores can in fact have a regulating impact on the population dynamics of *Carmichaelia* species, and could thus, cause their decline (Crawley 1983; Hendrix 1988; Watkinson 1986).

Reduced regeneration as a consequence of herbivory by introduced mammals has previously been observed for *Carmichaelia williamsii* and *C. australis* (Heenan and de Lange 1999), and also for snow tussock (Lee et al. 1993). However, while in these studies the underlying mechanisms remained uncertain, the combination of reduced regeneration with the drastically reduced seed production found in this study explained the nature of the impact.

The dynamics of the riverbed habitat of *C. juncea* make abundant seed production and regeneration essential for the persistence of this species (Speirs and Gurney 2001). With every flood, existing islands are washed away, while new surfaces establish. To ensure persistence in this habitat, *C. juncea* has to follow a 'bet-hedging strategy' (Stearns and Crandall 1981) by spatially spreading the risk of being washed away. The effects of the flood events during the trial period demonstrated this. As all caged plants flowered and seeded profusely, the three cages remaining at the end of the trial period contained abundant offspring. The only uncaged plot with relatively abundant regeneration was swept away, and in the three remaining plots only a single seedling was present at the end of the trial.

The effect of herbivory on plant populations depends strongly on the life-history of the plants, namely their longevity, the existence of a soil seed bank, and their dispersal strategies (Crawley 1983; Bastrenta et al. 1995; Louda and Potvin 1995). With the exception of *C. juncea*, *Carmichaelia* are probably relatively long-lived plants (Heenan 1997b), which together with their observed tolerance to browse, is likely to delay a potential population decline. Also, the level of browsing pressure, and hence, seed production may differ from year to year, allowing varying levels of regeneration. A further buffer for population decline is given by the longevity of *Carmichaelia* seeds (Crawley 1983; Grüner and Heenan 2001), with some seeds remaining dormant and viable in the soil for at least 18 months (Williams et al.

1996; I. Grüner, unpubl. data). Not enough is known about the dispersal strategies of *Carmichaelia* species to evaluate their role in the population dynamics of the species. While herbivory had a pronounced effect on *C. juncea* in the Waiho River, it did not affect the populations at the other three study sites. The lack of flowering and seed production of *C. hollowayi* did not appear to be caused by herbivory. I could not confirm the predation of flowers and seeds by rats as reported by Molloy et al. (1999b). *C. vexillata* showed no regeneration, despite abundant seed production. Instead, the pods and seeds remained on the ground besides the plants. These observations emphasise the need for a better understanding of the life-histories of the species and their ecological requirements, if we want to properly evaluate the impact of herbivory, and other factors, on the species.

6.5.5 Implications for Conservation Management

The results of the four exclosure trials illustrated that the impact of herbivory by introduced mammals on indigenous plants varies from species to species and from site to site. Therefore, the significance of browse as a threat to a plant population needs to be assessed for each individual case, and generalisation to other species or populations is questionable (Buxton et al. 2001). However, the results also demonstrated that herbivory by introduced mammals can pose a serious threat to the persistence of *Carmichaelia* populations. Furthermore, they allowed the identification of some of the processes by which the herbivores regulate the plant populations.

A detrimental effect on the survival of adult plants was not observed, but only ongoing monitoring could confirm this for longer periods of time. However, priority should be given to the study of the effects of herbivores on seedlings and juveniles, as these life stages are likely to be more sensitive to the impact (Hendrix 1988; Hulme 1996).

In the Waiho River, the inhibition of reproductive activity with resulting seed-limitation of regeneration was identified as a mechanism by which the introduced herbivores controlled the population of *C. juncea*. Although this situation was not found for the other species and populations, it is likely that higher browse intensities or more frequent events would lead to similar effects. One aim of the conservation management of *Carmichaelia* species, therefore, should be to minimise any reduction in fecundity on the plants.

The measures chosen to achieve this will vary from site to site. Cage-like or larger exclosures could be put in place, or animal pest control could be implemented to limit browsing pressure. However, before measures are taken, the actual impacts on the plants

need to be assessed to ensure targeted and efficient control (Forsyth et al. 2000). The trials illustrated that the presence of herbivores does not necessarily entail browse damage, and that the impact can vary over time, probably dependent on the availability of other food resources (Crawley 1983; Illius and O'Connor 2000). The methods used for the assessment of browse intensity need to be chosen very carefully to avoid altering effects caused by the assessments themselves (Cahill et al. 2001).

At two of the three sites where browse damage was observed, the active herbivores were hares. In the Mackenzie Basin their population density has increased substantially since the decline of the rabbit populations (Clout 2002; D. Woods, DoC Twizel, pers. comm.). Although detrimental impacts of hares on vegetation and plant species have frequently been reported (e.g., Flux 1967; Blay 1989; Rose and Platt 1992; Molloy and Clarkson 1996; Norton 2001), efficient control methods have not yet been developed (Wong and Hickling 1999; Forsyth et al. 2000). The impact of sheep on *C. hollowayi* at Awahokomo could easily be controlled by farm management.

Finally, the observed differences in vulnerability to browse depending on plant architecture could aid in priority setting for the conservation management of *Carmichaelia* species. Extrapolation of the findings to the other *Carmichaelia* species could help identifying the most vulnerable species, at least in relation to the vulnerability of their adults to suffer failure of seed production.

The results showed that, among the dwarf shrubs, openly branched species are more vulnerable to this threat than densely branched species. The openly branched *C. juncea* was considerably more affected than the densely branched *C. vexillata*, at least at the assessed browse intensities. The other dwarf shrub species, *C. hollowayi* and *C. astonii*, are therefore, also likely to be relatively vulnerable, as both species possess a relatively open and spreading growth habit. Among the shrub species, the sparsely branched *C. crassicaule* and *C. curta* are likely to be more vulnerable than the usually densely branched *C. australis*. The tree species *C. muritai* and *C. stevensonii*, and the climber *C. kirkii* are unlikely to be browsed to a degree where seed production is prevented. *C. kirkii* is protected by the dense growth of the divaricate shrubs it usually grows in, and adults of *C. muritai* and *C. stevensonii* are 6-7 m tall, with large crowns and abundant flowers.

7 Conservation Management of *Carmichaelia*

7.1 Introduction

Indicators for Vulnerability

The results of this study illustrated that the impact of introduced species on *Carmichaelia* species varies depending on their specific characteristics. For example, the severity of the impact of competition on the establishment of *Carmichaelia* varied depending on the habitat ecology of the species. In addition, the vulnerability of the species to shoot competition corresponded with the growth rate of juveniles and the maximum height of adult plants, while the vulnerability to root competition was associated with the length of the vessel elements in the wood. Chapter 6 illustrated that plant architecture determined the vulnerability of adult *Carmichaelia* to herbivory by introduced mammals.

The correlations between the characteristics of *Carmichaelia* species and their vulnerability to the impact of introduced plants and animals suggested that these species characteristics could be used as indicators for the vulnerability of species to these threats. The use of such indicators in the conservation management of threatened species would allow priorities to be set on the most vulnerable species, and management strategies could be developed, targeting the most significant threats for each species.

Grouping of Species

The observed correlations between species' characteristics and their vulnerability to the impact of introduced species further suggested that species with similar characteristics could be grouped together as having similar vulnerability, and therefore, similar management needs. Such a grouping of species has been previously suggested as a tool in threatened species conservation, as management plans dealing with several species at a time are likely to be more efficient than the traditional single-species approach (Franklin 1993; Tear et al. 1995; Clark and Harvey 2002). However, the criteria for the selection of appropriate groups are still largely unclear (Clark and Harvey 2002). The aim is to combine species that face similar threats, and therefore, have similar management needs (New 1999; Clark and Harvey 2002). In New Zealand, four out of ten plant recovery plans, currently published or in preparation, are multi-species plans. One of them uses taxonomic proximity as selection criterion (Norton and Grüner in prep.), while two others combine taxonomic proximity with

similarity in habitat ecology (Norton and de Lange 1999; Allen 2000). One plan selects species with similar habitat ecology and growth form (Jones 2002).

The results presented here, showed that taxonomic proximity is not necessarily a good indicator for similarity in the management needs of species. Although closely related, the *Carmichaelia* species differed widely in their vulnerability to the impact of introduced species. Habitat ecology, in contrast, proved to be a useful criterion, but only in relation to the impact of competition. The example of *C. crassicaule* and *C. vexillata* illustrated that similar habitat ecology does not necessarily imply similar vulnerability to impacts other than competition. Both species were characterised as grassland species (section 4.5.2), with similar vulnerability to competition (chapter 5), but while *C. crassicaule* seemed likely to be highly vulnerable to introduced herbivorous mammals, *C. vexillata* proved to be relatively resistant (chapter 6). Plant architecture appeared to be a more useful indicator than habitat ecology, in relation to the latter impact. Other growth form related traits were also useful in relation to shoot competition ('maximum plant height' in chapter 5), but they did not reflect the vulnerability of species to root competition.

Overall the findings of this study suggested that, while traits of species can be used as indicators for their vulnerability to threats, these traits are likely to vary with the threat factor considered. Given the wide range of factors affecting species in today's environment, the identification of species that are vulnerable to the same range of threats, therefore, becomes a multi-dimensional problem (c.f. Lawler et al. 2002).

Holt (1984) was the first to suggest that species are poised in multi-dimensional space, with some regions being closer to extinction than others. Conservation management aims at moving species from high risk areas into more favourable regions (Holt 1984). Using multivariate techniques, Given and Norton (1993) and Selvi (1997) analysed this 'space', with the axes being formed by a range of factors related to taxonomy, demography, species biology, and threatening impacts. The results describe distinct groups of species with similar 'threat profiles'. However, in both studies, the significance of threats, in particular that of extrinsic factors, is based on observations and assumptions, rather than reliable data, casting doubt on the validity of the attained grouping.

The results of the study presented here, suggested that the axes of the multidimensional space could be formed by species characteristics and the related vulnerability to potential threat factors. Such an analysis would result in groups of species with similar 'vulnerability profiles', and allow reliable inferences on the management needs of these species. Furthermore, this study provided variables, namely, habitat ecology, growth rate, maximum

height of adults, length of vessel elements in the wood, and plant architecture, that could be used in such analyses as indicators for the vulnerability of species to the impacts of competition and herbivory. The relative vulnerability of the *Carmichaelia* species to competition was further reflected by the competitive response rankings attained in the competition experiments (chapter 5).

Although the present study was restricted to the South Island of New Zealand and to only one genus of indigenous shrubs, the findings are likely to also apply to other genera and regions, as a number of studies have observed similar correlations between the identified characteristics and the vulnerability of species to competition (Grime and Jeffrey 1965; Grime 1979; Augspurger 1984; Carlquist 1988; Gaudet and Keddy 1988; Tilman 1988; Keddy and Shipley 1989; Williams and Buxton 1989; Rosch et al. 1997; Ebbett and Ogden 1998), and herbivory (Marquis 1996; Mc Intyre 1996; Hadar et al. 1999; Stowe et al. 2000). However, the outlier position of *C. kirkii* in the correlations of growth rate and plant height with tolerance to light competition indicated that such relationships are not necessarily valid across different growth forms (c.f., Lavorel et al. 1997).

Vulnerability Profiles of Carmichaelia *Species*

The New Zealand Department of Conservation currently prepares a multi-species recovery plan including all *Carmichaelia* species considered to be threatened in New Zealand at the present time (Norton and Grüner in prep.). The species are grouped together because of their taxonomic proximity. However, as outlined above, taxonomy is not necessarily a useful criterion for the grouping of species. This section, therefore, applies the principles discussed above to the ten *Carmichaelia* species studied, with the aim of identifying groups of species with similar vulnerability profiles, and to assess their usefulness in the planning of management strategies.

7.2 Methods

To develop a grouping of the *Carmichaelia* species, their vulnerability profiles were analysed in relation to four potential threats: shoot competition, root competition, herbivorous mammals, and habitat loss. Ideally, a wider range of threats, extrinsic as well as intrinsic, would be considered to identify groups with similar vulnerability profiles. However, as habitat loss and the impact of introduced species are believed to represent the major threats to indigenous plants in New Zealand today (Dopson et al. 1999), the results are likely to be highly relevant for the conservation management of *Carmichaelia* species.

Three variables were used as indicators for the vulnerability of the species to shoot and root competition, namely, the two response rankings attained in the competition experiments, and the length of vessel elements as an additional indicator for vulnerability to root competition (chapter 5; Table 7.1). Growth rate and maximum plant height were not included in the analysis, as the correlation between these variables and the vulnerability to competition did not apply to the climber *C. kirkii*. As *C. hollowayi* had not been included in the shoot competition trial, its vulnerability to shoot competition was estimated to be similar to that of *C. astonii*. This seemed legitimate, as both species occur in very similar habitats (chapter 4).

Table 7.1: Relative vulnerability of the *Carmichaelia* species to shoot and root competition, herbivory and habitat loss. V_{factor} – Vulnerability relating to this factor; lowest vulnerability = 1, highest vulnerability = 10; vessel length is positively correlated with vulnerability to root competition (chapter 5), for other variables see text.

Species	$V_{Shoot\ competition}$, ranking	$V_{Root\ competition}$, ranking	Vessel length, ranking	$V_{Herbivory}$	$V_{Habitat\ loss}$
C. astonii	7.5	3	1	8	9.5
C. australis	6	8	9.5	3	2
C. crassicaule	4	6	4.5	8	2
C. curta	9	4	4.5	8	4.5
C. hollowayi	7.5	1	2.5	8	9.5
C. juncea	10	7	6	8	4.5
C. kirkii	1	5	7.5	3	7
C. muritai	2	9	7.5	3	7
C. stevensonii	3	10	9.5	3	7
C. vexillata	5	2	2.5	3	2

Plant architecture served as indicator for the vulnerability of the species to herbivory by introduced mammals. The vulnerability of the species was rated as either low or high,

according to the discussion in chapter 6. The vulnerability of the species to habitat loss followed the ranking developed by Dopson et al. (1999).

To analyse the relationships between the various species and their vulnerability to the four threat factors, a principal component analysis was conducted, using the software package SAS 8.01 (SAS Institute Inc.).

7.3 Results

The first principal component was very strong (eigenvalue = 2.822), explaining 56.4% of the variability between the species. It was mainly determined by the vulnerability of the species to root competition, in interaction with their vulnerability to shoot competition and herbivory (Table 7.2). Species with high, positive values of the first principal component were characterised by high vulnerability to shoot competition and herbivory, but low vulnerability to root competition (*C. astonii*, *C. hollowayi*, Fig. 7.1). Conversely, species with low, negative values were characterised by high vulnerability to root competition, but comparatively low vulnerability to shoot competition and herbivory (*C. stevensonii*, *C. muritai*, *C. australis*, *C. kirkii*). Because of the interaction between the factors, species with intermediate values of the first principal component were characterised by either high or low vulnerability to all four threats.

Table 7.2: The first two principal components (Pcom) illustrating the vulnerability profiles of the *Carmichaelia* species. V_{factor} – Vulnerability relating to this factor.

	Pcom 1	**Pcom 2**
Eigenvalue	2.822	1.061
$V_{Shoot\ competition}$, ranking	0.438	0.474
$V_{Root\ competition}$, ranking	-0.491	0.202
Vessel length, ranking	-0.539	0.153
$V_{Herbivory}$	0.502	0.205
$V_{Habitat\ loss}$	0.158	-0.818
Variability explained	56.4%	21.2%

The second principal component was considerably weaker than the first (eigenvalue = 1.061), and mainly determined by the vulnerability of the species to habitat loss. Subsequent principal components were not considered, as they were comparatively weak.
The *Carmichaelia* species separated into four distinct groups (Fig. 7.1). *C. astonii* and *C. hollowayi* grouped closely together, both species being characterised by high vulnerability

to shoot competition, herbivory, and habitat loss, but relatively low vulnerability to root competition. The vulnerability profiles of *C. kirkii*, *C. muritai*, and *C. stevensonii* were characterised by relatively high vulnerability to root competition and habitat loss, but low vulnerability to shoot competition and herbivory. *C. crassicaule*, *C. curta*, *C. juncea*, and *C. vexillata* formed a third group, but the vulnerability profiles of these species were relatively variable. The species grouped together because of the interaction between the factors determining the first principal component. While *C. juncea* and *C. curta* were relatively vulnerable to all factors, in particular, to the impact of shoot competition and herbivory, *C. vexillata* was characterised by relatively low vulnerability to all factors (Table 7.1). *C. crassicaule* seemed to take an intermediate position, being close to *C. juncea* and *C. curta* in its higher vulnerability to root competition and herbivory, but similar to *C. vexillata* in its relatively low vulnerability to shoot competition and habitat loss. *C. australis* separated from all other species, showing relatively high vulnerability to root and shoot competition, but low vulnerability to the other factors.

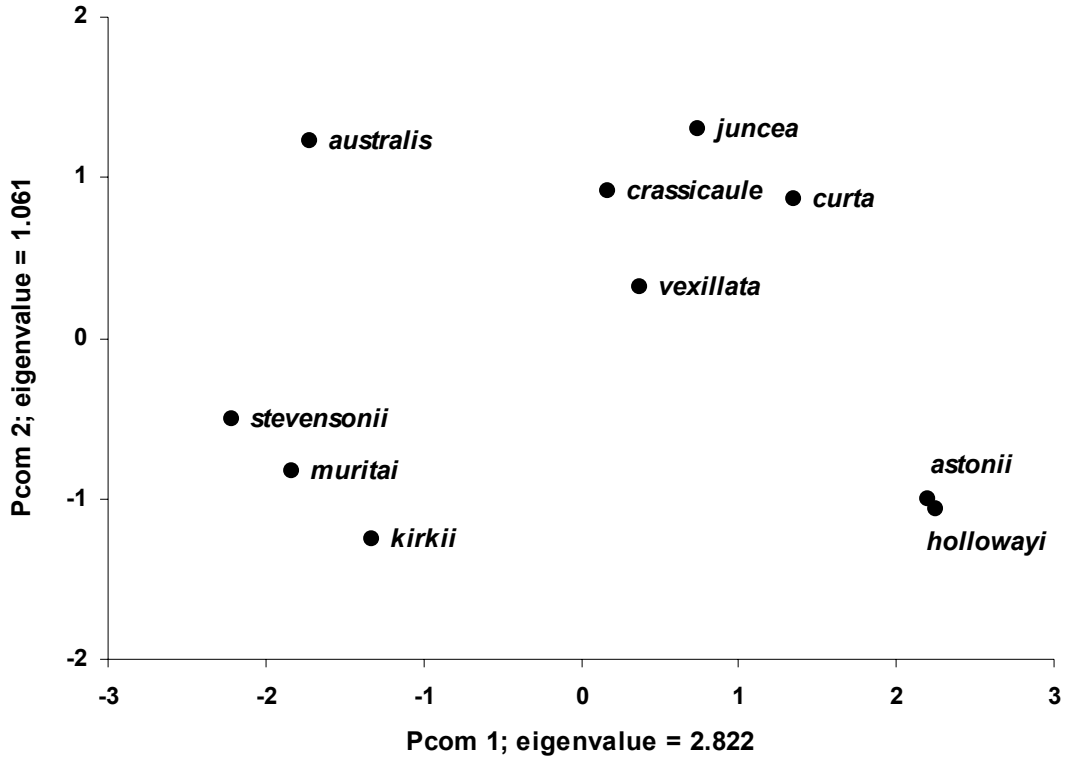


Fig. 7.1: Distribution of *Carmichaelia* species in relation to their vulnerability to the impacts of introduced species and habitat loss. Pcom – principal component.

7.4 Discussion

Grouping of Species

The results illustrated that multivariate analysis of the vulnerability profiles of threatened species can provide a useful tool to identify groups of species suitable for multi-species recovery planning. *C. astonii* and *C. hollowayi* represented one such group, *C. kirkii*, *C. muritai*, and *C. stevensonii* another, the species within each group being connected by similar vulnerability profiles. However, it also became clear that the results of such analyses have to be treated with caution. The example of the group comprising *C. crassicaule*, *C. curta*, *C. juncea*, and *C. vexillata* illustrated that the factors determining the axes of the multivariate space, and in particular, the interactions between these factors, need to be understood, as they can cause the grouping of species with widely different vulnerability profiles. However, consideration of the individual characteristics of species within such inhomogeneous groups can still allow the identification of species suitable for grouping. In the example here, *C. curta* and *C. juncea* could be grouped together, while *C. crassicaule* and *C. vexillata* were distinct and, therefore, should be treated separately.

C. australis was the only common species included in the analysis. This species is currently not considered in need of conservation management, as it occurs widespread and in a wide range of habitats (see chapter 4). Consistent with this distinct status, the vulnerability profile of *C. australis* separated this species from all other species. However, its relatively high vulnerability to shoot, and in particular, root competition seemed at odds with its status as common species. This inconsistency highlighted that the impact of introduced species is not the only factor responsible for the rarity of the other *Carmichaelia* species, but that other factors, extrinsic and intrinsic, are likely to also play a role.

The attained grouping of the *Carmichaelia* species corresponded largely with the ecological grouping of the species developed in chapter 4. This was not surprising as habitat ecology not only represented an indicator for the vulnerability of species to competition, but also for their vulnerability to habitat loss (Dopson et al. 1999). However, the example of *C. crassicaule* and *C. vexillata* illustrated that the grouping of species according to habitat ecology might not be satisfactory in all cases, depending on the influence of other threat factors. Both species are characterised as grassland species, but were separated in their vulnerability profiles mainly due to their contrasting vulnerability to herbivory.

The estimated vulnerability to competition referred to the impact of introduced plants on the seedling establishment of *Carmichaelia* species. As this is believed to be the decisive life-stage for the persistence of a population under competitive conditions (Goldberg 1996, Larcher 1995, Peart 1989), the estimated vulnerability is likely to reflect the likelihood of persistence of the *Carmichaelia* species. Vulnerability to herbivory, in contrast, referred to the vulnerability of adults, and the probability that seed production is inhibited by the impact. While successful seed production is an important component of functioning population dynamics, the vulnerability of juveniles and young adults to herbivory seems to be equally important, and should, therefore, be considered. However, the vulnerability of *Carmichaelia* at these early life-stages seemed to be high for all species, as browsed juveniles and young adults were repeatedly observed for all species (except *C. muritai,* for which no regeneration was found). Addition of this factor to the analysis, therefore, would not have altered the resulting grouping of the *Carmichaelia* species.

Significance of Threats

An understanding of the vulnerability profiles of threatened species allows the grouping of species with similar profiles, and based on this, enable the development of general management guidelines. However, the vulnerability profiles do not necessarily reflect which factors pose actual threats to the species in their current habitats and at the present time. The results of the previous chapters illustrated that, while species might be vulnerable to certain impacts, these factors need not be effective at the locality or time considered.

A discrepancy between the vulnerability profile of a species and the present relevance of a threat can arise as the result of displacement processes. For example, a number of indigenous species in New Zealand are thought to have been displaced from their original habitats due to their vulnerability to the impact of introduced species (Wardle 1991). The present habitats represent refuge sites at which competition with introduced plants or herbivory by introduced mammals are not effective, or at least occur with reduced intensity. Characteristically, these habitats are steep rock outcrops, impeding access by mammalian herbivores, or sites on infertile or shallow soils, limiting invasion by adventives (Wardle 1991; Milchunas and Noy-Meir 2002). Several *Carmichaelia* species are found in such habitats (e.g., *C. astonii*, *C. crassicaule*, *C. curta*; chapter 4), suggesting that their present distribution is at least partly the result of displacement processes, and that their vulnerability profiles do not necessarily correspond with the threats affecting the species in their current habitats. The significance of threat factors can further vary between sites, depending on the local resource levels. For example, herbivory by introduced mammals posed an immediate threat in the lowland populations of *C. juncea* in South Westland, but did not appear to threaten

this species at higher altitudes (Welcome Flat). This difference was likely to be the result of differences in the densities of herbivore populations and in the availability of other food resources (c.f. Crawley 1983; Blay 1989). The impact of competition is likely to vary in a similar way, depending on the degree of local invasion and resource availability. Evidence for this comes from a number of competition studies investigating the effects of competition in resource gradients (e.g., Wilson and Tilman 1991; Campbell and Grime 1992; Belcher et al. 1995; Brooks 2000).

A further difficulty in evaluating the significance of threats arises from their temporal variability. For example, the plants of *C. hollowayi* on top of the rock outcrop at Awahokomo showed signs of severe, and relatively recent browse in October 2000. However, no fresh browse was observed on these plants in the following two years (chapter 6), illustrating that herbivore impact at this site is variable over time. Similarly, herbivore impact on a *C. vexillata* population monitored during this study (chapter 6) varied seasonally, with stronger herbivore pressure during the winter months.

The evaluation of the current significance of threats to a species is further complicated by the fact that threats are not independent but interact. A number of studies show, for example, that the effect of root competition on plants depends on the level of shoot competition, and vice versa (e.g., Donald 1958; Wilson 1988; Wilson and Tilman 1991; Belcher et al. 1995; Casper and Jackson 1997; Schippers et al. 1999; Schippers and Kropff 2001; Cahill 2002). Similarly, the effects mammalian herbivores have on plants can vary with the level of plant competition at a site (e.g., Mc Laren 1996; Lentz and Cipollini 1998; Cabin et al. 2000; Meiners and Handel 2000; van der Wal et al. 2000).

These interactions also need to be considered, when management strategies for the conservation of threatened plants are developed, as the alleviation of one factor might exacerbate the impact of another. For example, reduced grazing pressure in grassland areas can lead to an increase in invasion by adventive plants, and thus, to higher levels of competition (Meurk et al. 1989; Edwards and Crawley 1999; Walker 2000). The same effect has been observed, when grazers were removed from scrub or forest communities, which they had previously damaged and opened up, facilitating invasion by weeds (Fox and Fox 1986).

The illustrated large spatial and temporal variability in the significance of threats implies that their actual significance needs to be evaluated for each species and each site, before any management can be implemented. This is necessary to ensure that the measures taken deal with currently relevant threat factors and that the most threatened populations of a species

are targeted. The vulnerability profiles developed from the characteristics of threatened species can guide such species and site-specific studies by pinpointing the most relevant threat factors to be examined. For example, the vulnerability profiles of *C. muritai*, *C. stevensonii*, and *C. kirkii* highlighted that an assessment of threats in habitats of these species should particularly focus on the presence of root competition and habitat loss rather than shoot competition or herbivory on adult plants, while all four factors are likely to be significant threats to *C. curta* and *C. juncea*.

Investigation of the current locations of the species before this background shows, for example, that *C. muritai* is particularly threatened in its persistence at Seaview, due to the intensive encroachment by exotic grasses at this site (chapter 4). The significance of herbivory as a threat to *C. juncea* varied between sites, demanding high priority for animal control in the lowland populations (chapter 6). Root and shoot competition in contrast did not appear to pose threats in the current populations of this species, however, these factors are likely to have caused extinctions in the past (chapter 4). A detailed evaluation of the significance of threats in the current habitats of the *Carmichaelia* species, based on their vulnerability profiles is provided in Appendix 5.

The example of the *Carmichaelia* species illustrates, that a combination of the general understanding of patterns in the vulnerability of species to threats with targeted species and site-specific studies is likely to be the most successful approach in the attempt to increase the efficiency of threatened species management.

8 Conclusions

The presented study contributed to a better understanding of the significance of introduced species as a threat to indigenous plants in New Zealand. In particular, the results highlighted some of the factors associated with the vulnerability of species to the impact of competition and herbivory. The vulnerability of the *Carmichaelia* species to competition varied depending on their habitat ecology and other species characteristics, in particular their growth rate and the length of their vessel elements (chapter 5). The impact of herbivory by introduced mammals varied in relation to the plant architecture of the *Carmichaelia* species (chapter 6).

The observed relationships between species traits and their vulnerability to threats provide useful tools for threatened species conservation, as they present a base for the identification of the most vulnerable species as well as the most significant threat factors. Low growing, openly branched species such as *C. juncea*, for example, proved distinctly more vulnerable to herbivory by introduced mammals than closely branched species such as *C. vexillata*. And while scrub and shrubland species were highly vulnerable to root competition, competition for light was unlikely to pose a threat to these species.

In addition, the characteristics related to the vulnerability of species provided a set of indicators that can be used to group species according to their vulnerability profiles. This grouping combines species that are likely to have similar management needs, and can therefore be used in multi-species recovery planning.

However, the example of the *Carmichaelia* species also illustrated that the assessment of vulnerability profiles alone is not sufficient for the planning of management strategies, as the vulnerability of species to a threat does not necessarily imply that this threat is actually active in the population of concern. The herbivory study (chapter 6) illustrated that the significance of threat factors can vary between populations of the same species, as well as over time. For example, while browse by introduced mammals posed a serious threat to *C. juncea* in the Waiho River, this threat was not effective in the Welcome Flat population during this study. Furthermore, threats that might have affected species in the past might not be active today due to changes in impact levels or the displacement of the indigenous species to refuge sites (see section 7.4 Significance of threats). Because of this variability in the impact of threat factors, the actual significance of threats needs to be assessed for each individual population before any management can be implemented, to ensure that the measures taken target currently active threats at each site. The attained vulnerability profiles can be used to guide such site-specific studies to focus on factors most likely to be relevant as threats to the species. An understanding of the relationships between species' characteristics and their

vulnerability to threats will, therefore, contribute to a more efficient approach in threatened species management than can be achieved by case studies alone.

Future research should aim at widening our understanding of the relationships between species' characteristics and their vulnerability to potential threats. A range of growth forms and species traits need to be investigated to identify meaningful patterns and ensure their relevance in different contexts. To achieve this a larger number of comparative studies is needed, analysing patterns across species. In addition, case-by-case studies should be based on a consistent methodology to allow the use of their results in comparative analyses. This would provide a chance to further increase our understanding of the general patterns and processes related to the decline and extinction of species.

9 References

Aarssen, L. W. and Keogh, T. 2002. Conundrums of competitive ability in plants: what to measure? - Oikos 96: 531-542.

Allan, H. H. 1982. Flora of New Zealand. Volume I. Indigenous tracheophyta. Psilopsida, lycopsida, filicopsida, gymnospermae, dicotyledones. - P. D. Hasselberg, Government Printer, Wellington.

Allen, R. B. 1992. RECCE. An inventory method for describing New Zealand's vegetative cover. - Forest Research Bulletin 181, Forest Research Institute, Christchurch.

Allen, R. B. 2000. Inland *Lepidium* recovery plan, 2000-2010. - Department of Conservation, Wellington.

Allen, R. B. and Mc Lennan, M. J. 1983. Indigenous forest survey manual: two inventory methods. - Forest Research Bulletin 48, Forest Research Institute, Christchurch.

Allen, R. B., Payton, I. J. and Knowlton, J. E. 1984. Effects of ungulates on structure and species composition in the Urewera Forests as shown by exclosures. - New Zealand Journal of Ecology 7: 119-130.

Arnold, G. W. 1964. Factors within plant associations affecting the behaviour and performance of grazing animals. - In: Crisp, D. J. (ed.) Grazing in terrestrial and marine environments. Blackwell Scientific Publications, Oxford, pp. 133-154.

Arnold, G. W., de Boer, E. S. and Boundy, C. A. P. 1980. The influence of odour and taste on the food preferences and food intake of sheep. - Australian Journal of Agricultural Research 31: 571-587.

Asher, G. W. 1979. Phenotypic variation and ecology of feral goat (*Capra aegagrus hircus* Couturier) populations in New Zealand. - MSc thesis, Victoria University, Wellington.

Asquith, N. M. 2001. Misdirections in conservation biology. - Conservation Biology 15: 345-352.

Atkinson, I. A. E. 1985. Derivation of mapping units for an ecological survey of Tongariro National Park North Island, New Zealand. - New Zealand Journal of Botany 23: 361-378.

Atkinson, I. A. E. 2001. Introduced mammals and models for restoration. - Biological Conservation 99: 81-96.

Atkinson, I. A. E. and Cameron, E. K. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. - Trends in Ecology & Evolution 8: 447-451.

Atkinson, I. A. E. and Greenwood, R. M. 1989. Relationships between moas and plants. - New Zealand Journal of Ecology 12 (Supplement): 67-95.

Atkinson, I. A. E. and Möller, H. 1990. Kiore. - In: King, C. M. (ed.) The handbook of New Zealand mammals. Oxford University Press, Oxford.

Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. - Journal of Ecology 72: 777-795.

Baars, R. and Kelly, D. 1996. Survival and growth responses of native and introduced vines in New Zealand to light availability. - New Zealand Journal of Botany 34: 389-400.

Bastrenta, B., Lebreton, J. D. and Thompson, J. D. 1995. Predicting demographic change in response to herbivory - a model of the effects of grazing and annual variation on the population-dynamics of *Anthyllis vulneraria*. - Journal of Ecology 83: 603-611.

Bazzaz, F. A. and Wayne, P. M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. - In: Caldwell, M. M. and Pearcy, R. W. (eds.) Exploitation of environmental heterogeneity by plants: ecophysiological processes above- and below-ground. Academic Press, San Diego, pp. 349-390.

Belcher, J. W., Keddy, P. A. and Twolan-Strutt, L. 1995. Root and shoot competition intensity along a soil depth gradient. - Journal of Ecology 83: 673-682.

Bellingham, P. J. 1998. Shrub succession and invasibility in a New Zealand montane grassland. - Australian Journal of Ecology 23: 562-573.

Bellingham, P. J., Walker, L. R. and Wardle, D. A. 2001. Differential facilitation by a nitrogen-fixing shrub during primary succession influences relative performance of canopy tree species. - Journal of Ecology 89: 861-875.

Benayas, J. M. R., Scheiner, S. M., Sanches-Colomer, M. G. and Levassor, C. 1999. Commonness and rarity: theory and application of a new model to mediterranean montane grasslands. - Conservation Ecology 3 (1): on-line.

Bevill, R. L. and Louda, S. M. 1999. Comparisons of related rare and common species in the study of plant rarity. - Conservation Biology 13: 493-498.

Bieleski, R. L. 1959. Factors affecting growth and distribution of kauri (*Agathis australis* Salisb.) I. Effect of light on the establishment of kauri and of *Phyllocladus trichomanoides* D. Don. - Australian Journal of Botany 7: 252-267.

Bilbrough, C. J. and Richards, J. H. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms of tolerance. - Ecology 74: 481-492.

Bishop, N. 1992. Natural history of New Zealand. - Hodder & Stoughton, Auckland.

Bishop, O. 1990. Wild flowers of New Zealand. - Hodder & Stoughton, Auckland.

Blay, G., J. 1989. Food preferences of the European hare (*Lepus europaeus* Pallas) on a fescue grassland. - MSc thesis, University of Canterbury, Christchurch.

Boyce, M. S. 1992. Population Viability Analysis. - Annual Review of Ecology and Systematics 23: 481-506.

Braun-Blanquet, J. 1964. Pflanzensoziologie. - Springer, Wien.

Brenstrum, E. 1999. The New Zealand weather book. - Craig Potton Publishing, Nelson.

Brooks, M. L. 2000. Competition between alien annual grasses and native annual plants in the Mojave Desert. - American Midland Naturalist 144: 92-108.

Brownsey, P. J. and Smith-Dodsworth, J. C. 1989. New Zealand ferns and allied plants. - David Bateman, Auckland.

Buxton, R. 1993. *Carmichaelia nigrans* - living on the edge. - New Zealand Botanical Society Newsletter 34: 6-7.

Buxton, R. P., Timmins, S. M., Burrows, L. E. and Wardle, P. 2001. Impact of cattle on Department of Conservation grazing leases in South Westland: results from monitoring 1989-1999, and recommendations. - Science for Conservation 179, Department of Conservation, Wellington.

Byers, D. L. and Meagher, T. R. 1997. A comparison of demographic characteristics in a rare and a common species of *Eupatorium*. - Ecological Applications 7: 519-530.

Cabin, R. J., Weller, S. G., Lorence, D. H., Flynn, T. W., Sakai, A. K., Sandquist, D. and Hadway, L. J. 2000. Effects of long-term ungulate exclusion and recent alien species control on the preservation and restoration of a Hawaiian tropical dry forest. - Conservation Biology 14: 439-453.

Cahill, J. F. 2002. Interactions between root and shoot competition vary among species. - Oikos 99: 101-112.

Cahill, J. F., Castelli, J. P. and Casper, B. B. 2001. The herbivory uncertainty principle: Visiting plants can alter herbivory. - Ecology 82: 307-312.

Calder, J. A., Wilson, J. B., Mark, A. F. and Ward, G. 1992. Fire, succession and reserve management in a New Zealand snow tussock grassland. - Biological Conservation 62: 35-45.

Caldwell, M. M., Eissenstat, D. M., Richards, J. H. and Allen, M. F. 1985. Competition for phosphorus: differential uptake from dual-isotope-labelled soil interspaces between shrub and grass. - Science 229: 384-386.

Caldwell, M. M., Richards, J. H., Manwaring, J. H. and Eissenstat, D. M. 1987. Rapid shifts in phosphate acquisition show direct competition between neighbouring plants. - Nature 327, 615-616.

Campbell, B. D. and Grime, J. P. 1992. An experimental test of plant strategy theory. - Ecology 73: 15-29.

Campbell, D. J. 1990. Changes in structure and composition of a New Zealand lowland forest inhabited by brushtail possums. - Pacific Science 44: 277-296.

Carlquist, S. 1988. Comparative wood anatomy. - Springer, Berlin.

Carlsen, T. M., Menke, J. W. and Pavlik, B. M. 2000. Reducing competitive suppression of a rare annual forb by restoring native Californian perennial grasslands. - Restoration Ecology 8: 18-29.

Casper, B. B. and Jackson, R. B. 1997. Plant competition underground. - Annual Review of Ecology and Systematics 28: 545-570.

Catovsky, S. and Bazzaz, F. A. 2002. Nitrogen availability influences regeneration of temperate tree species in the understory seedling bank. - Ecological Applications 12: 1056-1070.

Caughley, G. 1989. New Zealand plant-herbivore ecosystems past and present. - New Zealand Journal of Ecology 12: 3-10.

Caughley, G. 1994. Directions in conservation biology. - Journal of Animal Ecology 63: 215-244.

Charig, A. J. 1989. The Cretaceous-Tertiary boundary and the last of the dinosaurs. - Philosophical Transactions of the Royal Society of London Series B 325: 387-398.

Clark, J. A. and Harvey, E. 2002. Assessing multi-species recovery plans under the endangered species act. - Ecological Applications 12: 655-662.

Clarkson, B. D. and Clarkson, B. R. 1993. Ecology of an elusive endemic shrub, *Pittosporum obcordatum* Raoul. - New Zealand Journal of Botany 32: 155-168.

Clout, M. N. 2002. Ecological and economic costs of alien vertebrates in New Zealand. - In: Pimentel, D. (ed.) Biological invasions. Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, London, pp. 185-193.

Clout, M. N. and Hay, J. R. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests. - New Zealand Journal of Ecology 12: 27-33.

Clout, M. N. and Lowe, S. J. 2000. Invasive species and environmental changes in New Zealand. - In: Mooney, H. A. and Hobbs, R. J. (eds.) Invasive species in a changing world. Island Press, Washington, pp. 369-383.

Coates, D. J. and Atkins, K. A. 2001. Priority setting and the conservation of Western Australia's diverse and highly endemic flora. - Biological Conservation 97: 251-263.

Cochrane, C. H. 1994. Vegetation assessment and its implications for feral goat management in Isolated Hill Scenic Reserve, Southern Marlborough. - MSc thesis, University of Canterbury, Christchurch.

Cockayne, L. 1928. The vegetation of New Zealand. - Die Vegetation der Erde. Sammlung pflanzengeographischer Monographien 14, Wilhelm Engelmann, Leipzig.

Conner, L. N. and Conner, A. J. 1988. Seed biology of *Chordospartium stevensonii*. - New Zealand Journal of Botany 26: 473-475.

Connor, H. E. 1965. Tussock grasslands in the Middle Rakaia Valley, Canterbury, New Zealand. - New Zealand Journal of Botany 3: 261-276.

Coulter, J. D. 1966. Dry spells in New Zealand as a factor in plant ecology. - Proceedings of the New Zealand Ecological Society 13: 4-7.

Cowan, P. E. 1991. Effects of introduced Australian brushtail possums (*Trichosurus vulpecula*) on the fruiting of the endemic New Zealand nikau palm (*Rhopadostylis sapida*). - New Zealand Journal of Botany 29: 91-93.

Cowan, P. E. and Waddington, D. C. 1990. Suppression of fruit production of the endemic forest tree, *Elaeocarpus dentatus*, by introduced marsupial brushtail possums, *Trichosurus vulpecula*. - New Zealand Journal of Botany 28: 217-224.

Crawley, M. J. 1983. Herbivory. The dynamics of animal-plant interactions. - Studies in Ecology 10, Blackwell Scientific Publications, Oxford.

Cropper, S. C. 1993. Management of endangered plants. - CSIRO Publications, Melbourne.

Damon, R. A. J. and Harvey, W. R. 1987. Experimental design, ANOVA, and regresseion. - Harper & Row, New York.

D'Antonio, C. M., Hughes, R. F., Mack, M., Hitchcock, D. and Vitousek, P. M. 1998. The response of native species to removal of invasive exotic grasses in a seasonally dry Hawaiian woodland. - Journal of Vegetation Science 9: 699-712.

D'Antonio, C. M., Meyerson, L. A. and Denslow, J. 2001. Exotic species and conservation. - In: Soulé, M. E. and Orians, G. H. (eds.) Conservation Biology. Research priorities for the next decade. Island Press, Washington, pp. 59-80.

D'Antonio, C. M. and Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. - Annual Review of Ecology and Systematics 23: 63-87.

Davis, M. A., Wrage, K. J. and Reich, P. B. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. - Journal of Ecology 86: 652-661.

de Lange, P. J. 1991. Goats' and possums' effects on threatened North Island plants: a preliminary report. - Sience and Research Internal Report 111, Department of Conservation, Wellington.

de Lange, P. J., Heenan, P. B., Given, D. R., Norton, D. A., Ogle, C. C., Johnson, P. N. and Cameron, E. K. 1999. Threatened and uncommon plants of New Zealand. - New Zealand Journal of Botany 37: 603-628.

de Lange, P. J. and Norton, D. A. 1998. Revisiting rarity: a botanical perspective on the meanings of rarity and the classification of New Zealand's uncommon plants. - Royal Society of New Zealand, Miscellaneous Series 48: 145-160.

de Lange, P. J., Norton, D. A. and Crowcroft, G. M. 2000. Taxonomy, ecology, and conservation of *Atriplex billardierei* and *A. hollowa*yi (Chenopodiaceae) in Australasia. - New Zealand Journal of Botany 38: 551-567.

de Lange, P. J. and Silbery, T. 1993. Saving the shrubby tororaro (*Muehlenbeckia astonii* Petrii) - an urban approach to threatened plant conservation. - In: Froggatt, P. and Oates, M. (eds.) People, plants and conservation: botanic gardens into the 21st century. Royal New Zealand Institute of Horticulture, pp. 11-19.

de Mauro, M. M. 1994. Development and implementation of a recovery program for the federal threatened lakeside daisy (*Hymenoxys acaulis var. glabra*). - In: Bowles, M. L. and Whelan, C. J. (eds.) Restoration of endangered species. Conceptual issues, planning and implementation. Cambridge University Press, Cambridge, pp. 298-321.

Diamond, J. M. 1976. Island biogeography and conservation: strategy and limitations. - Science 193: 1027-1029.

Diamond, J. M. 1989a. Overview of recent extinctions. - In: Western, D. and Pearl, M. C. (eds.) Conservation for the twenty-first century. Oxford University Press, New York, pp. 37-41.

Diamond, J. M. 1989b. The present, past and future of human-caused extinctions. - Philosophical Transactions of the Royal Society of London Series B 325: 469-476.

Dierschke, H. 1994. Pflanzensoziologie: Grundlagen und Methoden. - Ulmer, Stuttgart.

Dierssen, K. 1990. Einführung in die Pflanzensoziologie. - Akademie-Verlag, Berlin.

Donald, C. M. 1958. The interaction of competition for light and for nutrients. - Australian Journal of Agricultural Research 9: 421-435.

Dopson, S. R., de Lange, P. J., Ogle, C. C., Rance, B. D., Courtney, S. P. and Molloy, J. 1999. The conservation requirements of New Zealand's nationally threatened vascular plants. - Threatened Species Occasional Publication 13, Department of Conservation, Wellington.

Druce, A. P. and Williams, P. A. 1989. Vegetation and flora of the Ben More - Chalk Range area of southern Marlborough, South Island. - New Zealand Journal of Botany 27: 167-199.

Dugan, P. 1993. Wetlands in danger - a world conservation atlas. - Oxford University Press, New York.

Duncan, R. P., Colhoun, K. M. and Foran, B. D. 1997. The distribution and abundance of *Hieracium* species (hawkweeds) in the dry grasslands of Canterbury and Otago. - New Zealand Journal of Ecology 21: 51-62.

Duncan, R. P., Webster, R. J. and Jensen, C. A. 2001. Declining plant species richness in the tussock grasslands of Canterbury and Otago, South Island, New Zealand. - New Zealand Journal of Ecology 25: 35-45.

Ebbett, R. L. and Ogden, J. 1998. Comparative seedling growth of five endemic New Zealand podocarp species under different light regimes. - New Zealand Journal of Botany 36: 189-201.

Ecroyd, C. E. 1996. The ecology of *Dactylanthus taylorii* and threats to its survival. - New Zealand Journal of Ecology 20: 81-100.

Edgar, E. and Connor, H. E. 2000. Flora of New Zealand. Volume V. Gramineae. - Manaaki Whenua Press, Lincoln.

Edwards, G. R. and Crawley, M. J. 1999. Herbivores, seed banks and seedling recruitment in mesic grassland. - Journal of Ecology 87: 423-435.

Ehrenfeld, D. W. 1970. Biological conservation. - Holt, Rinehart and Winston, New York.

Ehrlich, P. and Ehrlich, A. 1981. Extinction. The causes and consequences of the disappearance of species. - Random House, New York.

Eliason, S. A. and Allen, E. B. 1997. Exotic grass competition in suppressing native shrubland re-establishment. - Restoration Ecology 5: 245-255.

Fenner, M. 1978. A comparison of the abilities of colonisers and closed-turf species to establish from seed in artificial swards. - Journal of Ecology 66: 953-963.

Fiedler, P. L. and Ahouse, J. J. 1992. Hierarchies of cause: towards an understanding of rarity in vascular plant species. - In: Fiedler, P. L. and Subodh, K. J. (eds.) Conservation biology. The theory and practice of nature conservation and management. Chapman & Hall, New York, pp. 23-47.

Fitzgerald, B. M. and Gibb, J. A. 2001. Introduced mammals in a New Zealand forest: long-term research in the Orongorongo Valley. - Biological Conservation 99: 97-108.

Flux, J. E. C. 1967. Hare numbers and diet in an alpine basin in New Zealand. - Proceedings of the New Zealand Ecological Society 14: 27-33.

Forsyth, D. M., Parkes, J. P. and Hickling, G. J. 2000. A case for multi-species management of sympatric herbivore pest impacts in the central Southern Alps, New Zealand. - New Zealand Journal of Ecology 24: 97-103.

Foster, B. L. 1999. Establishment, competition and the distribution of native grasses among Michigan old-fields. - Journal of Ecology 87: 476-489.

Foufopoulos, J. and Ives, A. R. 1999. Reptile extinctions on land-bridge islands: life-history attributes and vulnerability to extinction. - American Naturalist 153: 1-25.

Fox, M. D. and Fox, B. J. 1986. The susceptibility of natural communities to invasion. - In: Groves, R. H. and Burdon, J. J. (eds.) Ecology of biological invasions. Cambridge University Press, Cambridge.

Frankel, O. H. and Soulé, M. E. 1981. Conservation and evolution. - Cambridge University Press, Cambridge.

Frankham, R. 1995. Conservation genetics. - Annual Review of Genetics 29: 305-327.

Franklin, J. F. 1993. Preserving biodiversity: species, ecosystems, or landscapes. - Ecological Applications 3: 202-205.

Freckleton, R. P. and Watkinson, A. R. 2000. Designs for greenhouse studies of interactions between plants: An analytical perspective. - Journal of Ecology 88: 386-391.

Freckleton, R. P. and Watkinson, A. R. 2001. Predicting competition coefficients for plant mixtures: reciprocity, transitivity and correlations with life-history traits. - Ecology Letters 4: 348-357.

Frost, L. C. 1981. The study of *Ranunculus ophioglossifolius* and its successful conservation at the Badgeworth Nature Reserve. - In: Synge, H. (ed.) The biological aspects of rare plant conservation. Wiley & Sons, Chichester, pp. 481-489.

Gaston, K. J. 1994. Rarity. - Population Community Biology Series 13, Chapman Hall, London.

Gaudet, C. L. and Keddy, P. A. 1988. Predicting competitive ability from plant traits: a comparative approach. - Nature 334: 242-243.

Gerry, A. K. and Wilson, S. D. 1995. The influence of initial size on the competitive responses of six plant species. - Ecology 76: 272-279.

Gibson, D. J., Connolly, J., Hartnett, D. C. and Weidenhamer, J. D. 1999. Designs for greenhouse studies of interactions between plants. - Journal of Ecology 87: 1-16.

Gill, B. and Martinson, P. 1991. New Zealand's extinct birds. - Random Century, Auckland.

Gillespie, T. W. 1999. Life history characteristics and rarity of woody plants in tropical dry forest fragments of Central America. - Journal of Tropical Ecology 15: 637-649.

Gilpin, M. E. and Soulé, M. E. 1986. Minimum viable populations: processes of species extinction. - In: Soulé, M. E. (ed.) Conservation biology. The science of scarcity and diversity. Sinauer, Sunderland, pp. 19-34.

Given, D. R. 1981. Threatened plants of New Zealand: Documentation in a series of islands. - In: Synge, H. (ed.) The biological aspects of rare plant conservation. Wiley & Sons, Chichester, pp. 67-79.

Given, D. R. 1994. Principles and practice of plant conservation. - Timber Press, Oregon.

Given, D. R. and Norton, D. A. 1993. A multivariate approach to assessing threat and for priority setting in threatened species conservation. - Biological Conservation 64: 57-66.

Godfray, H. C. J. and Crawley, M. J. 1998. Introductions. - In: Sutherland, W. J. (ed.) Conservation science and action. Blackwell Science, Oxford, pp. 39-65.

Goldberg, D. E. 1990. Components of resource competition in plant communities. - In: Grace, J. and Tilman, D. (eds.) Perspectives on plant competition. Academic Press, San Diego, pp. 27-49.

Goldberg, D. E. 1996. Competitive ability: Definitions, contingency and correlated traits. - Philosophical Transactions of the Royal Society of London Series B 351: 1377-1385.

Goldberg, D. E. and Fleetwood, L. 1987. Competitive effect and response in four annual plants. - Journal of Ecology 75: 1131-1143.

Goldberg, D. E. and Landa, K. 1991. Competitive effect and response hierarchies and correlated traits in the early stages of competition. - Journal of Ecology 79: 1013-1030.

Goodman, D. 1987. The demography of chance extinction. - In: Soulé, M. E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge, pp. 11-34.

Gordon, D. R., Welker, J. M., Menke, J. W. and Rice, K. J. 1989. Competition for soil water between annual plants and blue oak (*Quercus douglasii*) seedlings. - Oecologia 79.

Grace, J. B. 1990. On the relationship between plant traits and competitive ability. - In: Grace, J. B. and Tilman, D. (eds.) Perspectives on plant competition. Academic Press, San Diego, pp. 51-65.

Grace, J. B. 1995. On the measurement of plant competition intensity. - Ecology 76: 305-308.

Greenwood, R. M. and Atkinson, I. A. E. 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. - Proceedings of the New Zealand Ecological Society 24: 21-33.

Grime, J. P. 1979. Plant strategies and vegetation processes. - Wiley & Sons, Chichester.

Grime, J. P., Hodgson, J. G. and Hunt, R. 1988. Comparative plant ecology: a functional approach to common British species. - Unwin Hyman, London.

Grime, J. P. and Jeffrey, D. W. 1965. Seedling establishment in vertical gradients of sunlight. - Journal of Ecology 53: 621-642.

Gross, K. L. 1984. Effects of seed size and growth form on seedling establishment of six monocarpic perennial plants. - Journal of Ecology 72: 369-387.

Grove, P. 2001. The status of *Carmichaelia curta* in the Waitaki River catchment. - Canterbury Botanical Society Journal 35: 37-42.

Groves, R. H. 2002. The impact of alien plants in Australia. - In: Pimentel, D. (ed.) Biological invasions. Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, London, pp. 11-23.

Grüner, I. and Heenan, P. B. 2001. Viability and germination of seeds of *Carmichaelia* (Fabaceae) after prolonged storage. - New Zealand Journal of Botany 39: 125-131.

Hadar, L., Noy-Meir, I. and Perevolotsky, A. 1999. The effect of shrub clearing and grazing on the composition of a Mediterranean plant community: functional groups versus species. - Journal of Vegetation Science 10: 673-682.

Hall, G. M. J. 1992. PC - RECCE Vegetation inventory data analysis. - Forest Research Bulletin 182, Forest Research Institute, Christchurch.

Harrington, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. - Ecology 72: 1138-1149.

Harvey, P. H. and Pagel, M. D. 1991. The comparative method in evolutionary biology. - Oxford University Press, Oxford.

Healy, A. J. and Edgar, E. 1980. Flora of New Zealand. Volume III. Adventive cyperaceous, petalous and spathaceous monocotyledons. - P. D. Hasselberg, Government Printer, Wellington.

Hedge, S. G. and Ellstrand, N. C. 1999. Life history differences between rare and common flowering plant species of California and the British Isles. - International Journal of Plant Sciences 160: 1083-1091.

Hedrick, P. W., Lacy, R., C., Allendorf, F. W. and Soulé, M. E. 1996. Directions in conservation biology: Comments on Caughley. - Conservation Biology 10: 1312-1320.

Heenan, P. B. 1995. A taxonomic revision of *Carmichaelia* (Fabaceae-Galegae) in New Zealand (part I). - New Zealand Journal of Botany 33: 455-475.

Heenan, P. B. 1996a. Identification and distribution of the Marlborough pink brooms, *Notospartium carmichaeliae* and *N. glabrescens* (Fabaceae-Galegeae), in New Zealand. - New Zealand Journal of Botany 34: 299-307.

Heenan, P. B. 1996b. A taxonomic revision of *Carmichaelia* (Fabaceae-Galegeae) in New Zealand (part II). - New Zealand Journal of Botany 34: 157-177.

Heenan, P. B. 1997a. Heteroblasty in *Carmichaelia*, *Chordospartium*, *Corallospartium*, and *Notospartium* (Fabaceae-Galegeae) from New Zealand. - New Zealand Journal of Botany 35: 243-249.

Heenan, P. B. 1997b. Wood anatomy of the *Carmichaelia* (Fabaceae) complex in New Zealand. - New Zealand Journal of Botany 35: 395-415.

Heenan, P. B. 1998a. An emended circumscription of *Carmichaelia*, with new combinations, a key, and notes on hybrids. - New Zealand Journal of Botany 36: 53-63.

Heenan, P. B. 1998b. Phylogenetic analysis of the *Carmichaelia* complex, *Clianthus*, and *Swainsona* (Fabaceae), from Australia and New Zealand. - New Zealand Journal of Botany 36: 21-40.

Heenan, P. B. and de Lange, P. J. 1999. Reproductive biology, ecology and conservation of *Carmichaelia williamsii* (Fabaceae), a vulnerable legume from New Zealand. - Pacific Conservation Biology 5: 179-190.

Heenan, P. B., de Lange, P. J., Glenny, D. S., Breitwieser, I., Brownsey, P. J. and Ogle, C. C. 1999. Checklist of dicotyledons, gymnosperms, and pteridophytes naturalised or casual in New Zealand: additional records 1997- 1998. - New Zealand Journal of Botany 37: 629-642.

Hendrix, S. D. 1988. Herbivory and its impact on plant reproduction. - In: Lovett Doust, J. and Lovett Doust, L. (eds.) Plant reproductive ecology. Patterns and strategies. Oxford University Press, Oxford, pp. 246-263.

Higham, T., Anderson, A. and Jacomb, C. 1999. Dating the first New Zealanders: The chronology of Wairau Bar. - Antiquity 73: 420-427.

Hill, M. O. 1979. TWINSPAN - A FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. - Ecology and Systematics, Cornell University, Ithaca.

Hodgson, J. G. 1986a. Commonness and rarity in plants with special reference to the Sheffield flora. Part I: The identity distribution and habitat characteristics of the common and rare species. - Biological Conservation 36: 199-252.

Hodgson, J. G. 1986b. Commonness and rarity in plants with special reference to the Sheffield flora. Part II: Relative importance of climate, soils and land use. - Biological Conservation 36: 253-274.

Holdaway, R. N. 1989. New Zealand's pre-human avifauna and its vulnerability. - New Zealand Journal of Ecology 12: 11-25.

Holdaway, R. N. 1999. A spatio-temporal model for the invasion of the New Zealand archipelago by the Pacific rat *Rattus exulans*. - Journal of the Royal Society of New Zealand 29: 91-105.

Holdaway, R. N. and Jacomb, C. 2000. Rapid extinction of the moas (Aves: Dinornithiformes): model, test, and implications. - Science 287: 2250-2254.

Hollinger, D. Y. 1987. Photosynthesis and stomatal conductance patterns of two fern species from different forest understoreys. - Journal of Ecology 75: 925-935.

Holloway, J. T. 1950. Deer and the forests of western Southland. - New Zealand Journal of Forestry 6: 123-137.

Holt, S. J. 1984. Categorisation of threats to and status of wild populations. - In: Fitter, R. and Fitter, M. (eds.) The road to extinction. Problems of categorising the status of taxa threatened with extinction. IUCN, Madrid, pp. 19-30.

Horne, R. S. C. 1979. Seasonal and altitudinal variations in diet and abundance of the European hare (*Lepus europaeus* Pallas) in Tongariro National Park, New Zealand. - MSc thesis, Massey University, Palmerston North.

Howard, T. G. and Goldberg, D. E. 2001. Competitive response hierarchies for germination, growth, and survival and their influence on abundance. - Ecology 82: 979-990.

Hughes, J. G. 1975. What sheep eat on developed and undeveloped high country. - Tussock Grasslands and Mountainlands Institute Review 31: 20-30.

Hulme, P. E. 1996. Herbivory, plant regeneration, and species coexistence. - Journal of Ecology 84: 609-615.

Hunter, G. G. and Blaschke, P. M. 1986. The New Zealand Land Resource Inventory vegetation cover classification. - Water & Soil Miscellaneous Publication 101, National Water and Soil Conservation Authority, Wellington.

Illius, A. W. and O'Connor, T. G. 2000. Resource heterogeneity and ungulate population dynamics. - Oikos 89: 283-294.

Jablonski, D. 1995. Extinctions in the fossil record. - In: Lawton, J. H. and May, R. M. (eds.) Extinction rates. Oxford University Press, Oxford, pp. 25-44.

James, I. L. and Wallis, F. P. 1969. A comparative study of the effects of introduced mammals on Nothofagus forest at Lake Waikareiti. - Proceedings of the New Zealand Ecological Society 16: 1-6.

Jennersten, O. 1995. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. - In: Ehrenfeld, D. (ed.) Plant conservation. Readings from Conservation Biology. Society for Conservation Biology, Blackwell Science, Oxford, pp. 130-137.

Jesson, L., Kelly, D. and Sparrow, A. 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. - New Zealand Journal of Botany 38: 451-468.

Jones, C. 2002. Threatened grassy plants of dry fertile sites. - Department of Conservation, Wellington.

Karr, J. R. 1991. Avian survival rates and the extinction process on Barro Colorado Island, Panama. - Conservation Biology 4: 391-397.

Keddy, P. A. 2001. Competition. - Population and Community Biology Series 26, Kluwer Academic Publishers, Dordrecht.

Keddy, P. A., Fraser, L. H. and Wisheu, I. C. 1998. A comparative approach to examine competitive response of 48 wetland plant species. - Journal of Vegetation Science 9: 777-786.

Keddy, P. A. and Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. - Oikos 54: 234-241.

Kelly, D. and Skipworth, J. P. 1984. *Tradescantia fluminensis* in a Manawatu (New Zealand) forest: I. Growth and effects on regeneration. - New Zealand Journal of Botany 22: 393-397.

King, C. M. 1990. The Handbook of New Zealand mammals. - Oxford University Press in association with the New Zealand Mammal Society, Auckland.

Kobe, R. K., Pacala, S. W., Silander, J. A. and Canham, C. D. 1995. Juvenile tree survivorship as a component of shade tolerance. - Ecological Applications 5: 517-532.

Kosola, K. R. and Gross, K. L. 1999. Resource competition and suppression of plants colonizing early successional old fields. - Oecologia 118: 69-75.

Kunin, W. E. and Gaston, K. J. (eds.) 1997. The biology of rarity. Causes and consequences of rare-common differences. - Population and Community Biology Series, Chapman & Hall, London.

Lande, R. C. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. - American Naturalist 142: 911-927.

Lande, R. C. 1998. Anthropogenic, ecological, and genetic factors in extinction. - In: Mace, G. M., Balmford, A. and Ginsberg, J. R. (eds.) Conservation in a changing world. Cambridge University Press, Cambridge, pp. 29-51.

Larcher, W. 1995. Physiological plant ecology. Ecophysiology and stress physiology of functional groups. - Springer Verlag, Berlin.

Laurance, W. F. 1991. Ecological correlates of extinction proneness in Australian tropical rainforest mammals. - Conservation Biology 5: 79-89.

Lavorel, S., Mc Intyre, S., Landsberg, J. and Forbes, T. D. A. 1997. Plant functional classifications: from general groups to specific groups based on response to disturbance. - Trends in Ecology & Evolution 12: 474-478.

Lawler, J. J., Campbell, S. P., Guerry, A. D., Kolozsvary, M. B., O'Connor, R. J. and Seward, L. C. N. 2002. The scope and treatment of threats in endangered species recovery plans. - Ecological Applications 12: 663-667.

Lee, W. G. 2001. Do we have plant structural defences against large ratite browsers? Divarication revisited. - Proceedings of the New Zealand Ecological Society, 50th Jubilee Conference, pp. 39-40.

Lee, W. G., Fenner, M. and Duncan, R. P. 1993. Pattern of natural regeneration of narrow-leaved snow tussock *Chionochloa rigida* ssp. *rigida* in Central Otago, New Zealand. - New Zealand Journal of Botany 31: 117-125.

Lentz, K. A. and Cipollini, D. F. 1998. Effect of light and simulated herbivory on growth of endangered northeastern bullrush, *Scirpus ancistrochaetus* Schuyler. - Plant Ecology 139: 125-131.

Lesica, P. 1995. Demography of *Astragalus scaphoides* and effects of herbivory on population growth. - Great Basin Naturalist 55: 142-150.

Lesica, P., Leary, R. F., Allendorf, F. W. and Bilderback, D. E. 1995. Lack of genetic diversity within and among populations of an endangered plant, *Howellia aquatilis*. - In: Ehrenfeld, D. (ed.) Plant conservation. Society for Conservation Biology, Blackwell Science, London, pp. 164-171.

Leutert, A. 1988. Mortality, foliage loss, and possum browsing in southern rata (*Metrosideros umbellata*) in Westland, New Zealand. - New Zealand Journal of Botany 26: 7-20.

Lloyd, D. G. 1972. A revision of the New Zealand, subantarctic, and South American species of Cotula. Section Leptinella. - New Zealand Journal of Botany 10: 277-372.

Loope, L. L. and Medeiros, A. C. 1994. Impacts of biological invasions on the management and recovery of rare plants in Haleakala National Park, Maui, Hawaiian Islands. - In: Bowles, M. L. and Whelan, C. J. (eds.) Restoration of endangered species. Conceptual issues, planning and implementation. Cambridge University Press, Cambridge, pp. 143-158.

Lord, J. M. 1990. The management of *Poa cita* grassland by grazing. - New Zealand Journal of Ecology 13: 43-49.

Louda, S. M. and Potvin, M. A. 1995. Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. - Ecology 76: 229-245.

Mace, G. M., Baillie, J. E., Beissinger, S. R. and Redford, K. H. 2001. Assessment and management of species at risk. - In: Soulé, M. E. and Orians, G. H. (eds.) Conservation Biology. Research priorities for the next decade. Island Press, Washington, pp. 11-29.

Mack, R. N., Simberloff, D., Lonsdale, W. M., Evans, H., Clout, M. and Bazzaz, F. A. 2000. Biotic invasions: Causes, epidemiology, global consequences, and control. - Ecological Applications 10: 689-710.

Mark, A. F. 1989. Responses of indigenous vegetation to contrasting trends in utilization by red deer in two Southwestern New Zealand National Parks. - New Zealand Journal of Ecology 12 (supplement): 103-114.

Mark, A. F. and Adams, N. M. 1979. New Zealand alpine plants. - A. H. & A. W. Reed, Wellington.

Markham, J. H. and Chanway, C. P. 1996. Measuring plant neighbour effects. - Functional Ecology 10: 548-549.

Marquis, R. J. 1996. Plant architecture, sectoriality and plant tolerance to herbivores. - Vegetatio 127: 85-97.

Matsumura, C. and Washitani, I. 2000. Effects of population size and pollinator limitation on seed-set of *Primula sieboldii* populations in a fragmented landscape. - Ecological Research 15: 307-322.

May, R. M., Lawton, J. H. and Stork, N. E. 1995. Assessing extinction rates. - In: Lawton, J. H. and May, R. M. (eds.) Extinction rates. Oxford University Press, Oxford.

Mc Clintock, E. 1987. The displacement of native plants by exotics. - In: Elias, T. S. (ed.) Conservation and management of rare and endangered plants. Proceedings of a California conference on the conservation and management of rare and endangered plants. California Native Plant Society, Sacramento, pp. 185-188.

Mc Donald, D. and Norton, D. A. 1992. Light environments in temperate New Zealand podocarp rainforests. - New Zealand Journal of Ecology 16: 15-22.

Mc Glone, M. S. 1983. Polynesian deforestation of New Zealand: a preliminary synthesis. - Archeology in Oceania 18: 11-25.

Mc Glone, M. S. 2001. The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. - New Zealand Journal of Ecology 25: 1-15.

Mc Glone, M. S. and Basher, L. R. 1995. The deforestation of the upper Awatere catchment, Inland Kaikoura Range, Marlborough, South Island, New Zealand. - New Zealand Journal of Ecology 19: 53-66.

Mc Glone, M. S., Duncan, R. P. and Heenan, P. B. 2001. Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. - Journal of Biogeography 28: 183-198.

Mc Glone, M. S. and Moar, N. T. 1998. Dryland holocene vegetation history, Central Otago and the Mackenzie Basin, South Island, New Zealand. - New Zealand Journal of Botany 36: 91-111.

Mc Intyre, S. 1996. Comparison of a common, rare and declining plant species in the Asteraceae: possible causes of rarity. - Pacific Conservation Biology 2: 177-190.

Mc Laren, B. E. 1996. Plant-specific response to herbivory: Simulated browsing of suppressed balsam fir on Isle Royale. - Ecology 77: 228-235.

Mc Queen, D. R. 2000. Divaricating shrubs in Patagonia and New Zealand. - New Zealand Journal of Ecology 24: 69-80.

Meads, M. J. 1976. Effects of oppossum browsing on northern rata trees in the Orongorongo Valley, Wellington, NZ. - New Zealand Journal of Zoology 3: 127-139.

Meiners, S. J. and Handel, S. N. 2000. Additive and nonadditive effects of herbivory and competition on tree seedling mortality, growth, and allocation. - American Journal of Botany 87: 1821-1826.

Menges, E. S. 1990. Population viability analysis for a rare plant. - Conservation Biology 4: 52-62.

Meurk, C. D., Norton, D. A. and Lord, J. M. 1989. The effect of grazing and its removal from grassland reserves in Canterbury. - In: Norton, D. A. (ed.) Management of New Zealand's natural estate. Occasional Publication 1, New Zealand Ecological Society, Christchurch, pp. 72-75.

Milchunas, D. G. and Noy-Meir, I. 2002. Grazing refuges, external avoidance of herbivory and plant diversity. - Oikos 99: 113-130.

Moen, J. and Meurk, C. D. 2001. Competitive abilities of three indigenous New Zealand plant species in relation to the introduced plant *Hieracium pilosella*. - Basic and Applied Ecology 2: 243-250.

Molloy, B. P. J. 1963. Soil genesis and plant succession in the subalpine and alpine zones of Torlesse Range, Canterbury, New Zealand. - New Zealand Journal of Botany 1: 137-148.

Molloy, B. P. J. 1994. Observations on the ecology and conservation of *Australopyrum calcis* (Triticeae: Gramineae) in New Zealand. - New Zealand Journal of Botany 32: 37-51.

Molloy, B. P. J. and Clarkson, B. D. 1996. A new, rare species of *Melicytus* (Violaceae) from New Zealand. - New Zealand Journal of Botany 34: 431-440.

Molloy, B. P. J., de Lange, P. J. and Clarkson, B. D. 1999a. *Coprosma pedicellata* (Rubiaceae), a new species from New Zealand. - New Zealand Journal of Botany 37: 383-397.

Molloy, B. P. J., Edgar, E., Heenan, P. B. and de Lange, P. J. 1999b. New species of *Poa* (Gramineae) and *Ischnocarpus* (Brassicaceae) from limestone, North Otago, South Island, New Zealand. - New Zealand Journal of Botany 37: 41-50.

Moon, G. and Lockley, R. 1982. New Zealand's birds. - Heinemann, Auckland.

Moore, L. B. 1976. The changing vegetation of Molesworth Station, New Zealand, 1944 to 1971. - New Zealand Department of Scientific and Industrial Research Bulletin 217, DSIR, Wellington.

Moore, L. B. and Cranwell, L. M. 1934. Induced dominance of *Microlaena avenacea* (Raoul) Hook. f., in a New Zealand rain-forest area. - Records of the Auckland Institute and Museum 1: 219-238.

Morgan, M. D. and Norton, D. A. 1992. Growth response to light of *Carex inopinata* Cook, an endangered New Zealand sedge. - New Zealand Journal of Botany 30: 429-433.

Murray, B. R., Thrall, P. H., Gill, A. M. and Nicotra, A. B. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. - Austral Ecology 27: 291-310.

Naito, K. and Nakagoshi, N. 1995. The conservation ecology of *Iris rossii* Baker (Iridaceae), a threatened plant in rural Japan. - Journal of Plant Research 108: 477-482.

New, T. R. 1999. Limits to species focusing in insect conservation. - Annals of the Entomological Society of America 92: 853-860.

New Zealand Meteorological Service. 1983. Climate regions of New Zealand. - NZ Meteorological Service Miscellaneous Publications 174, Wellington.

New Zealand Meteorological Service. 2002. The climate of New Zealand. - NZ Meteorological Service (www.metservice.co.nz), on-line.

Newsome, P. F. J. 1987. The vegetative cover of New Zealand. - Water & Soil Miscellaneous Publication 112, National Water and Soil Conservation Authority, Wellington.

Norbury, G. 2001. Advances in New Zealand mammalogy 1990-2000: lagomorphs. - Journal of the Royal Society of New Zealand 31: 83-97.

Norton, D. A. 1991. Scientific basis for the conservation management of New Zealand plant communities. - In: Spellerberg, I. F., Goldsmith, F. B. and Morris, M. G. (eds.) The scientific management of temperate communities for conservation. Blackwell Science, London, pp. 349-381.

Norton, D. A. 1995a. *Trilepidea adamsii*: an obituary for a species. - In: Ehrenfeld, D. (ed.) Plant conservation. Society for Conservation Biology, Blackwell Science, London, pp. 52-57.

Norton, D. A. 1995b. Vegetation on goat-free islands in a low-alpine lake, Paparoa Range, and implications for monitoring goat control operations. - New Zealand Journal of Ecology 19: 67-72.

Norton, D. A. 2001. Re-establishment of the shrubby tororaro (*Muehlenbeckia astonii* Petrie), a nationally threatened plant. - Science & Research Internal Report 188, Department of Conservation, Wellington.

Norton, D. A. and Courtney, S. P. 2000. Vegetation and flora of Blue Duck Scientific Reserve, Kaikoura. - Canterbury Botanical Society Journal 34: 37-49.

Norton, D. A. and de Lange, P. J. 1999. Coastal cresses (nau) recovery plan. - Department of Conservation, Wellington.

Norton, D. A., de Lange, P. J. and Miller, C. 1998. *Carmichaelia juncea* - a little known plant on the brink of extinction. - New Zealand Botanical Society Newsletter 52: 11-13.

Norton, D. A. and Grüner, I. in prep. South Island threatened broom (*Carmichaelia*) recovery plan. - Department of Conservation, Wellington.

Norton, D. A., Hobbs, R. J. and Atkins, L. 1995. Fragmentation, disturbance, and plant distribution: mistletoes in woodland remnants in the Western Australian wheatbelt. - Conservation Biology 9: 426-438.

Norton, D. A., Lord, J. M., Given, D. R. and de Lange, P. J. 1994. Over-collecting: an overlooked factor in the decline of plant taxa. - Taxon 43: 181-185.

Norton, D. A. and Reid, N. 1997. Lessons in ecosystem management from management of threatened and pest Loranthaceous mistletoes in New Zealand and Australia. - Conservation Biology 11: 1-12.

Nugent, G., Fraser, W. and Sweetapple, P. 2001. Top down or bottom up? Comparing the impacts of introduced arboreal possums and 'terrestrial' ruminants on native forests in New Zealand. - Biological Conservation 99: 65-79.

Ogle, C. C., Cock, G. D., Arnold, G. and Mickleson, N. 2000. Impact of an exotic vine *Clematis vitalba* (Ranunculaceae) and of control measures on plant biodiversity in indigenous forest, Taihape, New Zealand. - Austral Ecology 25: 539-551.

Orians, G. H. and Soulé, M. E. 2001. Introduction. - In: Soulé, M. E. and Orians, G. H. (eds.) Conservation Biology. Research priorities for the next decade. Island Press, Washington, pp. 1-9.

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Kobe, R. K. and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis and dynamics. - Ecological Monographs 66: 1-43.

Parkes, J. P. and Thomson, C. 1995. Management of thar. - Science for Conservation 7, Department of Conservation, Wellington.

Parsons, M. J., Douglass, P. and Macmillan, B. H. 1998. Current names list for wild gymnosperms, dicotyledons and moncotyledons (except grasses) in New Zealand as used in Herbarium CHR. - Manaaki Whenua Press, Lincoln.

Pavlik, B. M. 1994. Demographic monitoring and the recovery of endangered plants. - In: Bowles, M. L. and Whelan, C. J. (eds.) Restoration of endangered species. Conceptual issues, planning and implementation. Cambridge University Press, Cambridge, pp. 322-350.

Pavlovic, N. B., de Mauro, M. and Bowles, M. 1992. Perspectives on plant competition - plant collection rate should be positively correlated with plant population size. - Plant Science Bulletin 38: 8-11.

Payton, I. J. 2000. Damage to native forests. - In: Montague, T. L. (ed.) The brushtail possum. Manaaki Whenua Press, Lincoln, pp. 111-125.

Peart, D. R. 1989. Species interactions in a successional grassland. - Journal of Ecology 77: 252-266.

Pekelharing, C. J., Frampton, C. M. and Suisted, P. A. 1998a. Seasonal variation in the impacts of brushtailed possums (*Trichosurus vulpecula*) on five palatable plant

species in New Zealand beech (*Nothofagus*) forest. - New Zealand Journal of Ecology 22: 141-148.

Pekelharing, C. J., Parkes, J. P. and Barker, R. J. 1998b. Possum (*Trichosurus vulpecula*) densities and impacts on fuchsia (*Fuchsia excorticata*) in South Westland, New Zealand. - New Zealand Journal of Ecology 22: 197-203.

Pfab, M. F. and Witkowski, E. T. F. 2000. A simple population viability analysis of the Critically Endangered *Euphorbia clivicola* RA Dyer under four management scenarios. - Biological Conservation 96: 263-270.

Pimm, S. L. 1998. Extinction. - In: Sutherland, W. J. (ed.) Conservation science and action. Blackwell Science, London, pp. 20-38.

Pimm, S. L., Jones, H. L. and Diamond, J. M. 1988. On the risk of extinction. - American Naturalist 132: 757-785.

Pimm, S. L., Russell, G. J., Gittleman, J. L. and Brooks, T. M. 1995. The future of biodiversity. - Science 269: 347-350.

Poole, A. L. 1951. Preliminary reports of the New Zealand-American Fiordland expedition. Investigations in Fiordland, New Zealand, in 1949. - New Zealand Department of Scientific and Industrial Research Bulletin 103, DSIR, Wellington.

Poole, A. L., West, C. J. and Adams, N. M. 1994. Trees and shrubs of New Zealand. - Manaaki Whenua Press, Lincoln.

Priantoro, T. A. 1995. An ecological study of the endemic prostrate broom (*Carmichaelia appressa* Simpson) at Kaitorete Spit, Canterbury, New Zealand. - MSc thesis, University of Canterbury, Christchurch.

Prince, S. D. and Hare, A. D. R. 1981. *Lactuca saligna* and *Pulicaria vulgaris* in Britain. - In: Synge, H. (ed.) The biological aspects of rare plant conservation. Wiley & Sons, Chichester, pp. 379-388.

Purdie, A. W. 1985. *Chordospartium muritai* (Papillionaceae) - a rare new species of New Zealand tree broom. - New Zealand Journal of Botany 23: 157-161.

Purvis, A., Gittleman, J. L., Cowlishaw, G. C. and Mace, G. M. 2000. Predicting extinction risk in declining species. - Proceedings of the Royal Society of London Series B 267: 1947-1952.

Pysek, P. and Prach, K. 1995. Invasion dynamics of *Impatiens glandulifera* - a century of spreading reconstructed. - Biological Conservation 74: 41-48.

Rabinowitz, D., Cairns, S. and Dillon, T. 1986. Seven forms of rarity and their frequency in the flora of the British Isles. - In: Soulé, M. E. (ed.) Conservation biology. The science of scarcity and diversity. Sinauer, Sunderland, pp. 182-201.

Reddiex, B. 1998. Diet selection of European rabbits (*Oryctolagus cuniculus*) in the semi-arid grasslands of the Mackenzie Basin, New Zealand. - MSc thesis, Lincoln University, Lincoln.

Riach, A. G. 1995. The tissue culture and selected physiology of *Chordospartium stevensonii*, a rare and endemic plant of New Zealand. - MSc thesis, University of Canterbury, Christchurch.

Ritchie, M. E., Tilman, D. and Knops, J. M. H. 1998. Herbivore effects on plant and nitrogen dynamics in oak savanna. - Ecology 79: 165-177.

Rodriguez, J. P. 2001. Exotic species introductions as a challenge for the conservation of South American biodiversity. - Interciencia 26: 479-485.

Rogers, G. M. 1991. Kaimanawa feral horses and their environmental impacts. - New Zealand Journal of Ecology 15: 49-64.

Rogers, G. M. 1996. Aspects of the ecology and conservation of the threatened tree *Olearia hectorii* in New Zealand. - New Zealand Journal of Botany 34: 227-240.

Rogers, G. M. and Walker, S. 2002. Taxonomic and ecological profiles of rarity in the New Zealand vascular flora. - New Zealand Journal of Botany 40: 73-93.

Rosch, H., van Rooyen, M. W. and Theron, G. K. 1997. Predicting competitive interactions between pioneer plant species by using plant traits. - Journal of Vegetation Science 8: 489-494.

Rose, A. B., Basher, L. R., Wiser, S. K., Platt, K. H. and Lynn, I. H. 1998. Factors predisposing short-tussock grasslands to *Hieracium* invasion in Marlborough, New Zealand. - New Zealand Journal of Ecology 22: 121-140.

Rose, A. B. and Frampton, C. M. 1999. Effects of microsite characteristics on *Hieracium* seedling establishment in tall- and short-tussock grasslands, Marlborough, New Zealand. - New Zealand Journal of Botany 37: 107-118.

Rose, A. B. and Platt, K. H. 1987. Recovery of Northern Fiordland alpine grasslands after reduction in the deer population. - New Zealand Journal of Ecology 10: 23-33.

Rose, A. B. and Platt, K. H. 1992. Snow tussock (*Chionochloa*) population responses to removal of sheep and European hare, Canterbury, New Zealand. - New Zealand Journal of Botany 30: 373-382.

Rose, A. B., Platt, K. H. and Frampton, C. M. 1995. Vegetation change over 25 years in a New Zealand short-tussock grassland: effects of sheep grazing and exotic invasions. - New Zealand Journal of Ecology 19: 163-174.

Rothmaler, W. 1994a. Exkursionsflora von Deutschland. Band 3. Gefässpflanzen: Atlasband. - Gustav Fischer Verlag, Jena.

Rothmaler, W. 1994b. Exkursionsflora von Deutschland. Band 4. Gefässpflanzen: Kritischer Band. - Gustav Fischer Verlag, Jena.

Schippers, P. and Kropff, M. J. 2001. Competition for light and nitrogen among grassland species: a simulation analysis. - Functional Ecology 15: 155-164.

Schippers, P., Snoeijing, I. and Kropff, M. J. 1999. Competition under high and low nutrient levels among three grassland species occupying different positions in a successional sequence. - New Phytologist 143: 547-559.

Schlesinger, W. H., Clark, J. S., Mohan, J. E. and Reid, C. D. 2001. Global environmental change: Effects on biodiversity. - In: Soulé, M. E. and Orians, G. H. (eds.) Conservation biology. Research priorities for the next decade. Island Press, Washington, pp. 175-223.

Scott, D., Dick, R. D. and Hunter, G. G. 1988. Changes in tussock grasslands in the central Waimakariri River basin, Canterbury, New Zealand, 1947-1981. - New Zealand Journal of Botany 26: 197-222.

Selvi, F. 1997. Rare plants on Mount Amiata, Italy: Vulnerability to extinction on an ecological 'island'. - Biological Conservation 81: 257-266.

Sessions, L. A. and Kelly, D. 2000. The effects of browntop (*Agrostis capillaris*) dominance after fire on native shrub germination and survival. - New Zealand Natural Sciences 25: 1-9.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. - BioScience 31: 131-134.

Shaffer, M. L. 1990. Population Viability Analysis. - Conservation Biology 4: 39-40.

Shaw, G. C. 1960. The New Zealand landscape. - In: Mc Lintock, A. H. (ed.) A descriptive atlas of New Zealand. R.E. Owen, Government Printer, Wellington, pp. 8-11.

Shaw, W. B. and Burns, B. R. 1997. The ecology and conservation of the endangered endemic shrub, kowhai ngutukaka *Clianthus puniceus* in New Zealand. - Biological Conservation 81: 233-245.

Simberloff, D. 1986. The proximate causes of extinction. - In: Raup, D. M. and Jablonski, D. (eds.) Patterns and processes in the history of life. Springer, Berlin, pp. 259-276.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. - Annual Review of Ecology and Systematics 19: 473-511.

Simberloff, D. 1998. Small and declining populations. - In: Sutherland, W. J. (ed.) Conservation science and action. Blackwell Science, London, pp. 116-134.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. - Forest Ecology and Management 115: 101-111.

Smale, M. C., Hall, G. M. J. and Gardner, R. O. 1995. Dynamics of kanuka (*Kunzea ericoides*) forest on South Kaipara Spit, New Zealand, and the impact of fallow deer (*Dama dama*). - New Zealand Journal of Ecology 19: 131-141.

Snedecor, G. W. and Cochran, W. G. 1989. Statistical methods. - Iowa State University Press, Ames.

Soulé, M. E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. - In: Soulé, M. E. and Wilcox, B. A. (eds.) Conservation biology. An evolutionary-ecological perspective. Sinauer, Sunderland, pp. 151-169.

Soulé, M. E. 1985. What is conservation biology? - BioScience 35: 727-734.

Soulé, M. E. 1986. Conservation biology and the 'Real World'. - In: Soulé, M. E. (ed.) Conservation biology. The science of scarcity and diversity. Sinauer, Sunderland, pp. 1-12.

Soulé, M. E. 1987. Introduction. - In: Soulé, M. E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge, pp. 1-10.

Southwood, T. R. E. and Henderson, P. A. 2000. Ecological methods. - Blackwell Science, Oxford.

Speirs, D. C. and Gurney, W. S. 2001. Population persistence in rivers and estuaries. - Ecology 82: 1219-1237.

Stearns, S. C. and Crandall, R. E. 1981. Bet-hedging and persistence as adaptation of colonisers. - In: Evolution today. Proceedings of 2nd international congress on systematics and evolution, pp. 371-384.

Stevens, G. R. 1980. New Zealand adrift. The theory of continental drift in a New Zealand setting. - Reed, Wellington.

Stewart, G. H., Wardle, J. A. and Burrows, L. E. 1987. Forest understorey changes after reduction in deer numbers, Northern Fiordland, New Zealand. - New Zealand Journal of Ecology 10: 35-42.

Stowe, K. A., Marquis, R. J., Hochwender, C. G. and Simms, E. L. 2000. The evolutionary ecology of tolerance to consumer damage. - Annual Review of Ecology and Systematics 31: 565-595.

Sturman, A. P. and Tapper, N. J. 1996. The weather and climate of Australia and New Zealand. - Oxford University Press, Oxford.

Tear, T. H., Scott, J. M., Hayward, P. H. and Griffith, B. 1995. Recovery plans and the endangered species act: Are criticisms supported by data? - Conservation Biology 9: 182-195.

Terborgh, J. and Winter, B. 1980. Some causes of extinction. - In: Soulé, M. E. and Wilcox, B. A. (eds.) Conservation biology: an evolutionary-ecological perspective. Sinauer, Sunderland, pp. 119-133.

Thornton, J. 1985. The Reed field guide to New Zealand geology. - Reed, Wellington.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. - Monographs in Population Biology, Princeton University Press, Princeton.

Timmins, S. M. and Reid, V. 2000. Climbing asparagus, *Asparagus scandens* Thunb.: a South African in your forest patch. - Austral Ecology 25: 533-538.

Treskonova, M. 1991. Changes in the structure of tall tussock grasslands and infestation by species of *Hieracium* in the Mackenzie Country, New Zealand. - New Zealand Journal of Ecology 15: 65-78.

Underwood, A. J. 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. - Cambridge University Press, Cambridge.

van der Wal, R., Egas, M., van der Veen, A. and Bakker, J. 2000. Effects of resource competition and herbivory on plant performance along a natural productivity gradient. - Journal of Ecology 88: 317-330.

van Gardingen, P. R. 1987. Environmental and stomatal physiology of *Nothofagus* seedlings. - PhD thesis, University of Canterbury, Christchurch.

Veblen, T. T. and Stewart, G. H. 1980. Comparison of forest structure and regeneration on Bench and Stewart Islands, New Zealand. - New Zealand Journal of Ecology 3: 50-68.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L., Rejmanek, M. and Westbrooks, R. 1997. Introduced species: A significant component of human-caused global change. - New Zealand Journal of Ecology 21: 1-16.

Vitousek, P. M., D'Antonio, C. M., Loope, L. L. and Westbrooks, R. 1996. Biological invasions as global environmental change. - American Scientist 84: 468-478.

Wagstaff, S. J., Heenan, P. B. and Sanderson, M. J. 1999. Classification, origins, and patterns of diversification in New Zealand Carmichaelinae (Fabaceae). - American Journal of Botany 86: 1346-1356.

Walck, J. L., Baskin, J. M. and Baskin, C. C. 1999. Relative competitive abilities and growth characteristics of a narrowly endemic and a geographically widespread *Solidago* species (Asteraceae). - American Journal of Botany 86: 820-828.

Walker, S. 2000. Post-pastoral changes in composition and guilds in a semi-arid conservation area, Central Otago, New Zealand. - New Zealand Journal of Ecology 24: 123-137.

Walker, S. and Lee, W. G. 2000. Alluvial grasslands in south-eastern New Zealand: vegetation patterns, long-term and post-pastoral change. - Journal of the Royal Society of New Zealand 30: 72-103.

Walker, S. and Lee, W. G. 2002. Alluvial grasslands of Canterbury and Marlborough, eastern South Island, New Zealand: vegetation patterns and long-term change. - Journal of the Royal Society of New Zealand 32: 113-147.

Walter, H. 1973. Vegetation of the earth in relation to climate and the eco-physiological conditions. - Springer Verlag, Berlin.

Wardle, D. A., Barker, G. M., Bonner, K. I. and Nicholson, K. S. 1998. Can comparative approaches based on plant ecophysiological traits predict the nature of biotic interactions and individual plant species effects in ecosystems? - Journal of Ecology 86: 405-420.

Wardle, K. 1999. The status of the endangered plants *Ischnocarpus novae-zealandiae* and *Carmichaelia kirkii* in the Wanaka Area. - Internal report, Department of Conservation, Dunedin.

Wardle, K. 2000a. The conservation status of *Carmichaelia kirkii* in the Mackenzie Basin. - Internal report, Department of Conservation, Christchurch.

Wardle, K. 2000b. The conservation status of *Carmichaelia vexillata* in the Mackenzie Basin. - Internal report, Department of Conservation, Christchurch.

Wardle, P. 1971. The forests and shrublands of the Seaward Kaikoura Range. - New Zealand Journal of Botany 9: 269-292.

Wardle, P. 1977. Plant communities of Westland National Park (New Zealand) and neighbouring lowland areas. - New Zealand Journal of Botany 15: 323-398.

Wardle, P. 1985. Environmental influences on the vegetation of New Zealand. - New Zealand Journal of Botany 23: 773-788.

Wardle, P. 1991. Vegetation of New Zealand. - Cambridge University Press, Cambridge.

Watkinson, A. R. 1986. Plant population dynamics. - In: Crawley, M. J. (ed.) Plant ecology. Backwell Scientific Publications, Oxford, pp. 137-184.

Webb, C. J., Sykes, W. R. and Garnock-Jones, P. J. 1988. Flora of New Zealand. Volume IV. Naturalised pteridophytes, gymnosperms, dicotyledons. - Botany Division, DSIR, Christchurch.

Whigham, D. F. and Chapa, A. S. 1999. Timing and intensity of herbivory: its influence on the performance of clonal woodland herbs. - Plant Species Biology 14: 29-37.

Widyatmoko, D. and Norton, D. A. 1997. Conservation of the threatened shrub *Hebe cupressoides* (Scrophulariaceae), eastern South Island, New Zealand. - Biological Conservation 82: 193-201.

Wilcox, B. A. 1980. Insular ecology and conservation. - In: Soulé, M. E. and Wilcox, B. A. (eds.) Conservation biology. An evolutionary-ecological perspective. Sinauer, Sunderland, pp. 95-117.

Williams, J. A. and West, C. J. 2000. Environmental weeds in Australia and New Zealand: issues and approaches to management. - Austral Ecology 25: 425-444.

Williams, P. A. 1982. Scenic reserves of Southern Marlborough Land District. - Biological Survey of Reserves 9, Department of Lands and Survey, Wellington.

Williams, P. A. 1989. Vegetation of the Inland Kaikoura Range, Marlborough. - New Zealand Journal of Botany 27: 201-220.

Williams, P. A. 1997. Ecology and management of invasive weeds. - Conservation Sciences Publication 7, Department of Conservation, Wellington.

Williams, P. A. and Buxton, R. P. 1989. Response to reduced irradiance of 15 species of native and adventive shrub and tree seedlings from eastern Canterbury. - New Zealand Journal of Ecology 12: 95-101.

Williams, P. A., Norton, D. A. and Nicholas, J. M. 1996. Germination and seedling growth of an endangered native broom, *Chordospartium muritai* A.W. Purdie (Fabaceae), found in Marlborough, South Island, New Zealand. - New Zealand Journal of Botany 34: 199-204.

Williams, P. A. and Timmins, S. 1990. Weeds in New Zealand protected natural areas. Review for the Department of Conservation. - Science and Research Series 14, Department of Conservation, Wellington.

Williams, P. A. and Timmins, S. 2002. Economic impacts of weeds in New Zealand. - In: Pimentel, D. (ed.) Biological invasions. Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, London, pp. 175-184.

Williamson, M. 1996. Biological invasions. - Population and Community Biology Series 14, Chapman & Hall, London.

Wilson, B. 1988. Shoot competition and root competition. - Journal of Applied Eccology 25: 279-296.

Wilson, C. M. and Given, D. R. 1989. Threatened plants of New Zealand. - DSIR Publishing, Wellington.

Wilson, H. D. 1994. Stewart Island plants. - Manuka Press, Christchurch.

Wilson, H. D. 1996. Wild plants of Mount Cook National Park. - Manuka Press, Christchurch.

Wilson, H. D. and Galloway, T. 1993. Small-leaved shrubs of New Zealand. - Manuka Press, Christchurch.

Wilson, S. D. and Keddy, P. A. 1986. Measuring diffuse competition along an environmental gradient, results from a shoreline plant community. - American Naturalist 127: 862-869.

Wilson, S. D. and Tilman, D. 1991. Components of plant competition along an experimental gradient of nitrogen availability. - Ecology 72: 1050-1065.

Wilson, S. D. and Tilman, D. 1995. Competitive responses of eight old-field plant species in four environments. - Ecology 76: 1169-1180.

Wiser, S. K., Allen, R. B. and Platt, K. H. 1997. Mountain beech forest succession after a fire at Mount Thomas Forest, Canterbury, New Zealand. - New Zealand Journal of Botany 35: 505-515.

Wong, V. and Hickling, G. J. 1999. Assessment and management of hare impact on high-altitude vegetation. - Science for Conservation 116, Department of Conservation, Wellington.

World Conservation Monitoring Centre. 1992. Global biodiversity: status of the earth's living resources: a report. - Chapman & Hall, New York.

World Conservation Monitoring Centre. 1998. 1997 IUCN red list of threatened plants. - The World Conservation Union, Gland.

Yockney, I. J. and Hickling, G. J. 2000. Distribution and diet of chamois (*Rupicapra rupicapra*) in Westland forests, South Island, New Zealand. - New Zealand Journal of Ecology 24: 31-38.

Ziswiler, V. 1967. Extinct and vanishing animals. - Springer Verlag, New York.

Zotov, V. D. 1938. Survey of the tussock-grasslands of the South Island, New Zealand. - New Zealand Journal of Science and Technology 20: 212-244.

Appendix 1

Records for Populations of the Ten Study Species

Map numbers and grid references are based on New Zealand Topographical Map Series 260 (1:50 000). The year of the most recent record is given for each location. Plant communities are given for locations visited as part of the habitat and plant community study (chapter 4); numbers refer to the respective headings of the community descriptions (see also fold-out overview in Appendix 2). 'Source' indicates the origin of the record; AK - Herbarium at the Auckland War Memorial Museum; CHR - Allan Herbarium, Landcare Research, Lincoln; DoC - Department of Conservation; IG - Ingrid Grüner; RARE - Rare plant collection held at Allan Herbarium, Landcare Research, Lincoln; WELT - Herbarium at Te Papa, Wellington. Numbers under 'Source' represent vegetation plots sampled for the habitat and plant community study (chapter 4); detailed plot records are available from the author upon request. The tables contain all records available for the *Carmichaelia* species from these sources in 2002, with the exception of *C. australis.* The records presented for this species are mainly restricted to the east of the South Island, as this represented the main study area.

At the end of Appendix 1, a transparency is provided, which can be used in connection with the distribution maps presented in section 3.3, to identify the mapsheets relevant for the marked locations.

C. astonii							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Ward	P29	0--	2--	2000		4.4.7a	WELT, CHR, 69-73
Near mouth of Flaxbourne River	P29	07-	28-	1975	Limestone rubble, steep hillside.		CHR
Flaxbourne River mouth	P29	08-	28-	1972			CHR
Ward	P29	04-	30-	1977			CHR
Isolated Hill	P29	8--	2--	1937			AK, WELT
Ure River on 'Brian Boru'	P29	881	221	-			WELT
Ure River, Isolated Hill	P29	902	227	-			CHR
North of Kekerengu, northwest of Mount Benmore	P29	91-	22-	1973	Cliff in gorge.		CHR
Isolated Hill	P29	914	243	2001		4.4.7b	142
Isolated Hill	P29	915	231	2001		4.4.7b	147-149
Isolated Hill	P29	916	240	2001		4.4.7b	143
Ure River	P29	928	253	1991	Rocky limestone face by stream.		CHR
North of Kekerengu, Mount Benmore	P29	93-	21-	1973	Rocks.		CHR
Waima River, upstream to Isolation Creek	P29	96-	24-	1983			RARE
Inland Kaikouras, Mead Gorge	P30	7--	1--	1916	Browsed.		CHR, AK, WELT
Southwest of Chalk Range, Mead Gorge	P30	75-	15-	1976	Limestone cliff.		CHR
Southwest of Chalk Range, Mead Hill	P30	77-	17-	1976	Limestone cliff.		CHR
Nearest major locality Clarence Point, on George Saddle	P30	719	998	1983			RARE
Southwest end of Chalk Range	P30	80-	18-	1976	Limestone cliff.		CHR
Swale Gorge, extends along length of gorge	P30	803	188	1983	1915: look browsed.		RARE, WELT

C. australis							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Makarora River	F38	08-	55-	1976			CHR
Lake Wanaka, Minaret Station	F39	0--	3--	1939	River flats.		CHR
Lake Wanaka, Makarora [River], Cameron Flat	G38	1--	6--	-	Forest edges.		CHR
Hunter Valley, near Billy Creek	G38	3--	6--	1961	River terrace.		CHR
Wanaka-Haast Rd	G40	115	199	2001		4.4.4.4	257
Welcome Flat	H36	587	283	2002			IG
Mount Cook, Mueller moraine"Hooker River, above lower swingbridge"Kitchener Creek"Hooker Valley, southern end	H36	7--	1--	1969	Scrubby bank. Colonised stony island in riverbed."		CHR
Mount Cook, near Hermitage	H36	75-	15-	1937	Old moraine.		CHR
South Canterbury, Tasman Valley, foot of Novara Spur	H36	8--	2--	1970	Stony vegetated shelf above shingle bank, below cliffs.		CHR
Hayman Rd	H37	856	827	2001		4.4.3.3a	232
South Canterbury, Ben Ohau Range, Glentanner Station	H37	7--	9--	1969	Stream side scrub, Twin Stream.		CHR
east side Tasman Valley, Mount Cook Station	H37	8--	0--	1963	Gully in morainic downs."Riverbank.		CHR
South Canterbury, Lake Pukaki, Tasman River bed, south east of Ferintosh	H37	81-	87-	1970	Shingle, now lake.		CHR
Lake Pukaki, east side, Tasman Downs.	H37	84-	85-	1975	Grassland near Lake.		CHR
Lake Pukaki, east side, Tasman Downs, Boltons Gully.	H37	85-	82-	1975			CHR
between Lakes Tekapo and Pukaki, (Guide Hill)	H37	89-	86-	1966	Modified tussock grassland.		CHR
Lake Ohau	H38	557	635	2001		4.4.3.3b	231
Lake Ohau, Maitland Stream	H38	5--	6--	1943	Riverbed.		CHR
Head of Lake Ohau	H38	55-	64-	1976			CHR
Head of Lake Ohau	H38	55-	65-	1983			CHR
Taieri County, Taieri Ferry	H45	8--	5--	1911			CHR
Havelock River, Carneys Creek	I35	249	438	1985	Scattered bushes in Chionochloa rigida tussocklands.		CHR
Two Thumb Range, Forbes River	I35	21-	47-	1991	Shrubland on fan.		CHR

Macauley River, Third Waterfall Stream	I36	196	245	1985	In shrublands (matagouri, Coprosma species) on gullysides.		CHR
Godley [River], near mouth of Mckinnon Stream	I36	0--	3--	1971	Short tussock grassland, developed on edge of riverflat in sheltered corner.		CHR
South Canterbury, Godley [River], Rutherford Stream	I36	0--	3--	1971	Foot of slope of dense Chionochloa flavescens.		CHR
Mt John	I37	061	885	2001		4.4.3.2	235
South Canterbury, Lake Tekapo, Mount John, DSIR Trial site	I37	062	885	1982	Growing among rocks on steep slope.		CHR
Lilybank Rd	I37	100	885	2001		4.4.3.2	236
South Canterbury, western foot of Two Thumb Range	I37	130	847	1985	Tussockland.		CHR
Lake Tekapo, Round Hill	I37	199	059	1996	In short tussock land.		CHR
Lake Tekapo, near hotel	I37	0--	8--	1939	Abundant along shores and riverbanks. "Lake shore." "Subprostrate on waters edge."		CHR
Tekapo	I37	04-	86-	-	Near lake.		CHR
Lake Tekapo, Lilybank Road	I37	09-	85-	1976			CHR
Lake Tekapo, Round Hill	I37	17-	06-	1993	Near lake.		CHR
Mackenzie Pass	I38	159	653	2000		4.4.4.4	54
Mackenzie Pass	I38	159	653	2000		4.4.3.2	55
Hakataramea Pass Summit	I38	163	521	1976			CHR
Burkes Pass	I38	180	769	1981			CHR
Mackenzie Pass	I38	201	653	2001		4.4.3.3c	140
Hakataramea Pass	I38	16-	51-	1976			CHR
South Canterbury, stream immediately north of MacKenzie Pass	I38	19-	64-	1978	South aspect slope.Tussock grassland by stream. Growing in scrubby tussock. On drier sites with short tussock on hillsides and adjacent terraces.		CHR
Mackenzie Pass	I38	19-	65-	1994			CHR
MacKenzie Pass, Lockharts Stream.	I38	22-	64-	1976			CHR
Lockharts Stream	I38	22-	65-	1976			CHR
Rollesby Valley Road, Coolgardie	I38	22-	70-	1976			CHR
Burkes Pass	I38	22-	77-	1975			CHR
Mt Dalgety	I39	195	484	2001		4.4.3.2	178

Mt Dalgety	I39	204	484	2001		4.4.3.2	176
Mt Dalgety	I39	204	484	2001		4.4.3.2	177
Hakataramea Pass Rd	I39	208	480	2000		4.4.4.4	59
Hakataramea Pass Rd	I39	242	366	2001		4.4.3.2	175
MacKenzie Basin, Hakataramea Pass Road	I39	14-	47-	1976			CHR
Hakataramea Valley, Cattle Creek	I39	22-	30-	1976			CHR
Haldon Station.	I39	92-	46-	1975			CHR
Awahokomo	I40	021	083	2001		4.4.6.1	83
near Kurow	I40	0--	0--	1940	Roadside.		CHR
near Waitaki Hydro	I40	05-	09-	1937	Stony river terrace.		CHR
Waitaki Valley, Gards Road	I40	12-	95-	1976			CHR
Lake Aviemore	I40	91-	13-	1976	Roadside.		CHR
Rangitata Valley, Erewhon Park, Jumped Up Downs	J35	357	409	1971	Common in fescue tussock.		CHR
South Canterbury, Lawrence Valley, junction of stream below Chowbok	J35	445	618	1977	Moraine, fellfield and herbfield, frequent at 3500ft.		CHR
Havelock Valley, Two Thumb Range	J35	30-	40-	1991	Riverbank shrubland.		CHR
Rakaia River, Lake Stream gorge	J35	58-	63-	1985	Scattered bushes in shrubland.		CHR
Lake Heron, Cameron fan	J35	60-	45-	1985	Scattered bushes in drier areas of toe of Cameron fan.		CHR
Dogs Range	J36	527	391	1968			CHR
Rangitata Valley	J36	617	158	1968	Roadside.		CHR
Ashburton River, South Branch, hillside above Blowing Point	J36	651	282	1978	"Grassland.		CHR
Rangitata Gorge Road.	J36	---	---	1979			CHR
Rangitata [River], Mesopotamia Station, approximately 1.6 km before cattleyards	J36	4--	2--	1968	Bank above roadside cutting.		CHR
Lake Camp.	J36	5--	3--	1975			CHR
Lake Emily, nearby hill.	J36	66-	37-	1975			CHR
Mid Canterbury, North Branch Hinds River, Mount Somers, Inverary	J36	69-	23-	1971	Shaded by matagouri, coprosma and olearia.		CHR
South [Branch] Ashburton River.	J36/ J37	---	---	1975			CHR
Kowhai Ridge, Te Moana Gorge	J37	512	828	2001		4.4.4.4	184
Mount Peel, Lynn Creek.	J37	66-	04-	1975			CHR

Waihi Gorge	J37			1980	Open grassland.		CHR
9 miles north of Pleasant Point	J38	---	---	-	Limestone rocks.		CHR
Pareora Gorge	J38	4--	5--	-			CHR
Timaru-Fairlie Road, Raincliff	J38	4--	6--	1938			CHR
Hanging Rock	J38	53-	66-	1981			CHR
7 miles north of Pleasant Point	J38	6--	6--	-	On limestone rocks.		CHR
Geraldine	J38	6--	7--	1938	Roadside.		CHR
South Canterbury, Hunters Hills, Otaio River	J39	450	295	1972	River gorge with limestone outcrop.		CHR
Hunters Hills	J39	---	---	-	Creek.		CHR
South Canterbury, Upper Pareora Gorge, south east of Dalziel homestead.	J39	3--	4--	1979	In steep wet subalpine grassland on talus, side of gorge. Scattered.		CHR
South Canterbury, Hunter Hills, Weaner Run	J39	41-	31-	1972	Open face tussock slope.		CHR
South Canterbury, Hunters Hills, Blue Cliffs Station	J39	47-	28-	1976	Steep-sided gully, lightly wooded.		CHR
near Waimate	J40	5--	0--	1938	On roadside.		CHR
Main North Road at Waitaki River bridge	J41	6--	8--	-			CHR
Arthur's Pass, bank of Bealy River above township	K33	9--	0--	1937	River flat.		CHR
Arthur's Pass	K33	9--	0--	1937	Subalpine scrub.		CHR
West Coast Road, near Paddy's Bend	K34	044	977	-			CHR
Cass, Mountain Biological Station	K34	082	965	1966	Beside Firebreak Road between Lake Sarah and hut.		CHR
Upper Rakaia River, Hydra Swamp.	K34	737	703	1981	On drier sites in the Chionochloa rubra bog on low river terrace.		CHR
Broken River Basin, Porter River Bridge	K34	0--	7--	-	Grassland and scrub		CHR
Porter River	K34	0--	7--	1917			CHR
Craigieburn	K34	0--	8--	1977			CHR
Selwyn County, Jordon River	K34			1945	Rocky bank.		CHR
Rakaia River Gorge	K35	013	424	2001		4.4.5.1	238
near Colgate, Birch View	K35	066	455	1968	On shaded bank along stream above waterfall.		CHR
Porters Pass	K35	075	669	1996	Loose shingle		CHR
South-facing slope in the lower reaches of Coach Stream	K35	095	663	1995	Occasional shrubs in a shrub community dominated by matagouri with Cytisus scoparius and tussock.		CHR

Mt Barker	K35	970	604	2000		4.4.4.4	61
Rakaia River, Double Hill Road.	K35	---	---	1976			CHR
Rakaia River, Zig Zag Road.	K35	0--	4--	1975			CHR
Island at Rakaia Gorge	K35	0--	4--	1938			CHR
Windwhistle	K35	0--	4--	1938	Roadside.		CHR
Lake Lyndon	K35	0--	6--	-	Grassland.		CHR
Rakaia Valley, Snowdon, High Peak Road	K35	02-	47-	1975			CHR
Rockwood Range	K35	03-	46-	1975			CHR
Birchview	K35	07-	44-	1975			CHR
Rockwood Bush, 8 km north east of Rakaia Gorge	K35	09-	45-	1968	Nothofagus solandri forest.		CHR
Broken River Basin, Coleridge Pass	K35	9--	6--	-			CHR
Lake Coleridge, Harper Road	K35	9--	6--	1975			CHR
Coleridge Pass	K35	9--	6--	1975			CHR
Lake Georgina	K35	9--	6--	1956			CHR
Lake Coleridge	K35	95-	61-	1976	Power Station intake.		CHR
Lyndon Road	K35	96-	61-	1975			CHR
Mount Somers, Blondin Stream, Inverary Street	K36	708	251	1972	Wet swamp.		CHR
Mount Somers, Woolshed Creek.	K36	7--	1--	1982	At creeksides, usually in alluvial soils.		CHR
Mid Canterbury, Mount Somers, Inverary", Limestone Hill, above Blondins Stream"	K36	71-	24-	1970	On hill, clay slip on lower slopes above stream.		CHR
Mid Canterbury, Mount Somers, Woolshed Creek	K36	75-	24-	1971	On banks of creek shaded by pittosporum and broadleaf.		CHR
Alford Forest.	K36	8--	3--	1978			CHR
Pudding Hill Stream.	K36	9--	3--	1978			CHR
South Canterbury, Ealing	K37	8--	8--	1962	Dry stony roadside.		CHR
Carew, Jones Road	K37	81-	89-	1970	Roadside.		CHR
about 11 km south west of Ashburton on Maronan Road	K37	9--	9--	1975	In browntop.		CHR
near Timaru, Kings Gully	K39			1944			CHR
Washdyke	K39			-			CHR
North of Timaru, near showgrounds	K39			-			CHR
near Timaru	K39			1939	On sand dunes - burned over.		CHR
West Amuri, Doubtful River, Clump Tree Flat	L32	4--	5--	1938	Among river terrace scrub.		CHR

North Canterbury, Lake Sumner, Lake Katrine	L32	43-	31-	1970			CHR
Lake Taylor	L33	476	259	2001		4.4.4.4	244
Poulter River	L33	1--	0--	1976			CHR
0.5km south of Poulter Bridge, terrace face	L34	211	953	1989	Open scrub on terrace face facing south.		CHR
Waimakariri Gorge, lower gorge opposite Smuggler Cove	L34	233	757	1971	Rocky bluffs by backwater directly below staircase"."		CHR
Mount Oxford, Dobson Stream	L34	321	784	1994	Growing on terrace scarp not far above creek in open forest edge; mountain beech forest.		CHR
Mount Torlesse	L34	1--	7--	1949			CHR
Poulter Gorge, prominent rock bluff, by power line	L34	20-	95-	1989	Crevices of rock bluff.		CHR
Ashley River, near Gorge	L34	4--	7--	1947	At banks near the gorge. Shade leaves.		CHR
Lees Valley, Ashley Gorge	L34	42-	84-	1975	Red tussock; damp. "Tussock slope."		CHR
Rockwood Stream	L35	102	464	1982			CHR
Waimakariri Gorge, at Woodstock	L35	253	684	1966	Rocky bank, more or less shaded by Sophora.		CHR
Eastern slopes of Rockwood Range, Rakaia, Brockley"	L35	1--	4--	1962	Short tussock grassland - degraded.		CHR
Malvern Hills, Hood's Bush.	L35	1--	4--	1980			CHR
Kowai River, below Porters Pass	L35	1--	6--	1969	River bed.		CHR
Kowai River, below Porters Pass	L35	1--	6--	1999			IG
Hood's Bush Scenic Reserve.	L35	13-	46-	1977			CHR
Selwyn River, gorge	L35	15-	54-	1974			CHR
North west of Kowai Bush	L35	21-	68-	1970	Edge of stream.		CHR
Oxford, View Hill	L35	32-	64-	1942			CHR
Kirwee, Main road west from Christchurch	L35	4--	4--	-			CHR
south of Oxford, Burnt Hill	L35	4--	5--	1956	Fescue tussock grassland.		CHR
1.6 km south of Oxford, Kennedy Road	L35	44-	53-	1970	Roadside scrub.		CHR
Ellesmere County, Bankside Reserve	L36	424	195	1970	Short tussock grassland.		CHR
Rockwood, Dunsandel Road.	L36	---	---	1975			CHR
Te Pirita	L36	20-	29-	1976			CHR
Te Pirita, Saunders Road.	L36	25-	28-	1975			CHR
Rakaia, on main road	L36	3--	1--	-			CHR

Te Pirita, Mitchells Road.	L36	30-	24-	1976			CHR
Bankside Railway Reserve	L36	40-	18-	1970	Roadside.		CHR
Bankside Reserve	L36	41-	19-	1976	Short tussock grassland.		CHR
Killinchy	L36	45-	18-	1970	Kanuka shrubland.		CHR
[North of Ashburton], east side Highway 1, 1.5 miles (2.4 km) north of Stanley Road	L37	1--	0--	1969			CHR
Wakanui, Five Star Beef property	L37	17-	85-	1994			CHR
Rakaia Island.	L37	40-	00-	1975	Rocky crevices.""		CHR
Lewis River	M31	60-	60-	1982			CHR
Lewis Pass, Dans Bridge.	M31	60-	69-	-			CHR
Clarence Valley, Mount Saint Patrick, Amuri Ski Basin	M31	8--	6--	1972	Beech forest in Williams Valley.		CHR
North Canterbury, Williams Valley, Mount St Patrick	M31	89-	62-	1975	Stream bank, forest margin.		CHR
Doubtful River	M32	5--	5--	1946	confluence!		CHR
West of Hanmer, Doubtful River	M32	5--	5--	1940			CHR
North Canterbury, Waiau River Valley, few miles west Hanmer turn off, Gabriels Gully	M32	8--	4--	1973	Scrub on dry rocky hillside.		CHR
North Branch Hurunui River near proposed damsite	M33	5--	2--	1979	Gorgy rock on sunny face.		CHR
Lake Sumner Road	M33	6--	1--	1975			CHR
North Canterbury, west of Hawarden, Lake Summner Road, Jacks Saddle	M33	64-	17-	1970			CHR
West of Hawarden, North Branch Waipara River,	M33	7--	0--	1962	Bank of creek.		CHR
Weka Pass	M33	85-	00-	1975	Grassland and scrub. Roadside."		CHR
North Canterbury, east of Waikari, Carvossa""	M33	87-	03-	1978	Undeveloped Notodanthonia scrub slope, on rock outcrops.		CHR
North Canterbury, Waipara River	M34	774	937	1967	Riverflat.		CHR
Head of Lees Valley	M34	51-	92-	1975			CHR
North Canterbury, Loburn Downs	M34	7--	7--	1959	Roadside.		CHR
Ashley Forest	M34	7--	7--	1970	Road bank.		CHR
Waipara Gorge	M34	7--	9--	1972	On steep grass and rock slopes, dry.		CHR
North Branch Waipara River, Broxton Road.	M34	72-	99-	1975			CHR
Leithfield	M34	8--	7--	1939	Roadside.		CHR

near Amberley	M34	8--	8--	1938	Roadside.		CHR
Weka Pass	M34	8--	9--	1941	Stream side.		CHR
North Canterbury, Lower Waipara, South Dean	M34	8--	9--	1986	Limestone scarp face.		CHR
Near Waipara, Hanmer Road	M34	8--	9--	1937	Grassland.		CHR
Amberley	M34	87-	82-	1975			CHR
Okuku River	M34/35	6--	8--	-			DoC
Near Eyrewell State Forest, Poyntz Road	M35	528	576	1969	Roadside.		CHR
Yaldhurst Road	M35	628	451	1961	Roadside, very shingly soil.		CHR
Christchurch, Heathcote-Avon Estuary, just south of Avon River bridge	M35	881	424	1976	In scrub of Plagianthus divaricatus.		CHR
Eyrewell Scientific Reserve	M35	4--	5--	1970	Margins of kanuka scrub.		CHR
Eyrewell Forest	M35	5--	5--	2001			IG
On Oxford side of Swannanoa, Tram Road	M35	5/6--	6--	1960	On roadside with matagouri.		CHR
Canterbury Plains, Halkett, NCCB Reserve	M35	52-	47-	1970	On dunes.		CHR
Paparua County, [Christchurch], four miles west of Yaldhurst	M35	6--	4--	1961	On depauperate sheep grazed pasture, on old river gravel (greywacke) with introduced grasses.		CHR
Old West Coast Road, past Chatterton Road.	M35	61-	45-	1975			CHR
Tram Road, Swannanoa	M35	67-	59-	1975			CHR
Conservators Road, Waimakariri River	M35	69-	46-	1975			CHR
Yaldhurst, School Road	M35	70-	43-	1975			CHR
Christchurch, Harewood	M35	71-	47-	1970	Danthonia grassland. "Scattered plants on dunes."		CHR
Harewood	M35	73-	47-	1975			CHR
Canterbury Plains, Pleasant Point foreshore	M35	8--	4--	1970	Stable sand dunes.		CHR
between Sockburn and Prebbleton	M36	712	360	1955	Wasteland at edge of old gravel pit.		CHR
Port Hills, below western summit, The Tors	M36	852	351	1986	Rocky ground with silver tussock, pasture and shrubs.		CHR
Banks Peninsula, Orton Bradley Park	M36	868	265	1996	Loess covered hillside - scattered trees and shrubs.		CHR
Lake Tennyson	M36	882	116	2001		4.4.5.2	182
Banks Peninsula, Little River	M36	897	125	1969	Roadside, tussock-grassland covered hills.		CHR

Leeston-Rakaia Highway.	M36	---	---	-			CHR
Springston-Leeston Road, Irwell junction	M36	5--	2--	1970	Roadside, with brown top and cocksfoot.		CHR
Springston	M36	6--	2--	1966	Waste land by gravel pit.		CHR
3.6 km south west of Templeton, Robinsons Road	M36	6--	3--	1962	Short grass, roadside.		CHR
South of Christchurch, Templeton	M36	6--	3--	-	On roadside.		CHR
Christchurch, Halswell Quarry	M36	75-	32-	-			CHR
Hallswell Quarry	M36	75-	33-	1975			CHR
Motukarara	M36	77-	19-	1975			CHR
Banks Peninsula, Prices Valley	M36	8--	1--	1955			CHR
Banks Peninsula, Lyttelton Harbour, Quail Island	M36	8--	3--	1977	Dry sunny slopes above cliffs on the north-east coastline. Poa caespitosa/Muehlenbeckia community. "Kanuka/Coprosma scrub around pond on the north-west."		CHR
Cashmere Hills	M36	8--	3--	1911			CHR
Port Hills, Lyttelton	M36	8--	3--	1954	Grassland near Victoria Park.		CHR
Kaituna Valley	M36	83-	18-	1976			CHR
Lake Forsyth.	M36	88-	10-	1975			CHR
Kaitorete Spit	M37	75-	09-	1994	In open droughty pasture.		CHR
Wairewa County, 10 miles west of Poranui on the Kaitorete Spit	M37	86-	09-	1961	On the landward side of the sand dunes with Muehlenbeckia astonii.		CHR
Upper Wairau, Wash Bridge.	N29	178	433	1977	Dense manuka scrub.		CHR
[Junction] Leatham River and Branch River	N29	239	425	1975			CHR
Branch River between Goat Stream & Fuchsia Stream	N29	252	443	1986	Open shrubland on terrace.		CHR
Wairau Valley	N29	19-	43-	1987	River cliff.		CHR
Junction Leatham River and Branch River	N29	2--	3--	1948	River flat.		CHR
Confluence of Branch River and Wairau River	N29	2--	4--	1971	On river terrace.		CHR
Leatham Valley	N29	27-	37-	1976	Grassland, hillside.		CHR
Lower Wairau Valley, Black Valley Stream	N29	97-	34-	1977			CHR
Upper Awatere [River], Molesworth Stream	N30	2--	0--	1943			CHR
Upper Awatere [River], Robinson Creek	N30	2--	9--	-			CHR
Molesworth, below farm paddocks	N30	28-	99-	1952			CHR

Clarence River, Hassock Corner, on B. Molloy's plot	N31	06-	66-	1969			CHR
North Canterbury, Mount Terako	N31	2--	6--	1970	Ridge by scree slope.		CHR
Tributary of Clarence River, near Bush Gully	N31	9--	6--	-	Streamside.		CHR
Mason River	N32	195	498	1983			CHR
Mason River	N32	259	579	1983	Abundant on terraces above river.		CHR
Wairau Valley, near Countess Stream	N32	983	329	1962	Roadside.		CHR
	N32	0--	3--	2001			IG
North Canterbury, between Waiau and Rotherham	N32	0--	3--	-			CHR
slopes of Mount Percival	N32	0--	5--	1950	Edge of beech forest.		CHR
Waiau, Rotherham Road	N32	06-	37-	1975			CHR
North Canterbury, Mason River	N32	1--	3--	1961	confluence!		CHR
	N32	1--	3--	2001			IG
North Canterbury, between Waiau and Rotherham	N32	1--	3--	1962	Hillside.		CHR
	N32	1--	4--	2001			IG
Lottery River, Waiau	N32	1--	4-- confluence	1956	Grassland of river terrace.		CHR
North Canterbury, near Waiau, Ngawiro Station	N32	17-	33-	1980	Scrub, streamside.		CHR
Whales Back	N32	2--	5--	1983			CHR
Kaikoura-Hanmer Rd	N32	29-	58-	2001		4.4.4.4	243
Hanmer Plains	N32	9--	5--	1877			CHR
Jacks Pass	N32	95-	56-	1975			CHR
North Canterbury, Headwaters of Blythe River, Kilmarnock Downs""	N33	2--	0--	1944	Scrub.		CHR
North Canterbury, Headwaters of Blythe River, Kilmarnock Downs""	N33	2--	0--	-	In scrub along headwaters of river.		CHR
North Canterbury, Napenape Scenic Reserve, 3km south of mouth of Blythe River on coast	N33	29-	06-	1974	On gravel cap on limestone at south end of reserve.		CHR
Hurunui River, near hotel	N33	9--	1--	1941			CHR
Hurunui River Bridge	N33	90-	14-	1983			CHR
North Canterbury, Motunau River	N34	151	962	1960			CHR

Motunau Road	N34	10-	95-	1983			CHR
Waipara, Limestone Creek	N34	9--	9--	1943			CHR
Waipara, Mt Cass Rd	N34	9--	9--	2001		4.4.4.4	CHR, 75
Waipara, Limestone Range	N34	9--	9--	1941	On hill slopes.		CHR
Little River, Kinloch Rd	N36	929	109	2001		4.4.4.4	181
Godley Head	N36	933	348	2000		4.4.5.2	60
Banks Peninsula, Okains Bay	N36	1--	2--	1965	On grass covered slopes, dominant shrub. "Coastal cliff."		CHR
near Little River	N36	9--	1--	-	Grassy banks.		CHR
Lighthouse Gully, [Banks Peninsula, gully below Godley Head]	N36	94-	35-	1972	Steep grass slopes.		CHR
Banks Peninsula, Valley above Big Bay	N36	99-	30-	1987	Scrubby bush and treeland on bluffy ground.		CHR
Banks Peninsula, Fishermans Bay	N37	16-	07-	1975			CHR
Banks Peninsula, Te Oka [Bay] Road	N37	9--	0--	-			CHR
Banks Peninsula, Peraki, east side of bay.	N37	95-	03-	1985	Top of eroded loess bank on coastal slope.		CHR
Tinline River	O27	5--	8--	1964			CHR
Rai River	O27	5--	9--	1947	Rocky bank.		CHR
Pelorus Bridge	O27	57-	89-	1989	Rocks beside river.		CHR
below bridge at foot of Rai Saddle, Brown's Reserve	O27	57-	99-	1943			CHR
Pelorus River	O27	58-	89-	1989	In open forest on river terrace.		CHR
Lower Waihopai Valley, near Avon Valley	O28	63-	51-	1981			CHR
Avon Valley	O29	579	384	2000		4.4.4.6	47
Awatere Valley, Jordan [River]	O29	6--	2--	1926			CHR
Upper Awatere Valley, Hodder River	O29	6--	2--	1954	Rocky face.		CHR
Tone Valley	O30	445	001	2000		4.4.6.4	29, 30
Tone Valley	O30	446	006	2000		4.4.4.5b	31
Tone Valley	O30	447	006	2000		4.4.4.1	33
Tone Valley	O30	450	011	2000		4.4.4.1	32
Yeo Stream, South Branch	O30	3--	9--	1996	Rocky bluff.		CHR
Upper Awatere River, near Molesworth Homestead	O30	31-	01-	1943			CHR
Tone Valley	O30	4--	0--	1984			CHR
Awatere Valley, Langridge	O30	4--	1--	1938			CHR

Langridge	O30	44-	12-	-	Terrace slope. East of Shingly Range.		CHR
Inland Kaikoura Range, west of Mitre Peak, east foot of Mount Lookout	O30	51-	09-	1983	Shrubland.		CHR
Awatere Valley, Upcott Saddle	O30	52-	19-	1975	Shrub-tussock land.		CHR
Inland Kaikoura Range, Awatere Valley, at foot of Mount Gladstone	O30	55-	18-	1983	Scrubland.		CHR
Inland Kaikoura Range, Totara Stream	O30	56-	12-	1983	Stream bank.		CHR
Kaikoura Range, Totara Stream	O30	57-	13-	1983	Stream bank.		CHR
Conway River	O31	327	603	2001		4.4.5.3	242
Charwell River	O31	398	651	2001		4.4.5.3	241
Hapuku Valley	O31	634	813	2001		4.4.4.2	239
Hapuku Valley	O31	643	817	2001		4.4.4.2	240
Jordan Stream Reserve	O31	695	865	1975	Bluff scrub on river margin.		CHR
Charwell River, near school - inland road between Waiau and Kaikoura	O31	39-	64-	1968	Modified tussock grassland.		CHR
Seaward Kaikoura Range, Upper Kowhai River	O31	5--	7--	1967	Beside stream.		CHR
North Canterbury, hills east of Parnassus, above Beltana Stream, near Radio Station	O32	388	328	1969	Grazed hilly tussock country with bush remnant in gullies and on ridges.		CHR
North Canterbury, hills east of Parnassus, above Beltana Stream, near Radio Station	O32	389	338	1969	Grazed hilly tussock country with bush remnant in gullies.		CHR
East Hundalee Hills, Okarahia Stream	O32	471	517	1968	Stream side bank.		CHR
South of Conway River	O32	---	---	1947			CHR
Leader River	O32	3--	3--/4--	1941	On river bed.		CHR
Whales Back, (Waiau - Kaikoura Road)	O32	30-	59-	1969	Scrub on roadside bank.		CHR
Kaikoura/Waiau Road, south of Conway River.	O32	34-	32-	1975			CHR
Conway River, State Highway 1	O32	37-	41-	1975			CHR
North Canterbury, Conway Flat	O32	4--	4--	1964	Shade.		CHR
Hundalee Hills	O32	4--	4--	-			CHR
near mouth of Conway River, Conway Flat	O32	47-	41-	1975			CHR
Gore Bay	O33	351	155	2001		4.4.5.2	74
North Canterbury, north of Hurunui River, Gore Bay	O33	3--	1--	1958			CHR
Point Robinson Road and Road to Hurunui River Mouth	O33	3--	1--	1962	Short tussock grassland.		CHR

Puangiangi Island	P25	929	479	1981	Coastal forest and scrub.		CHR
Titi Island	P26	059	279	1981	Coastal forest.		CHR
French Pass	P26	804	311	1968	Roadside bank.		CHR
Pelorus Sound, Maud Island	P26	85-	19-	1971	Coastal scrub.		CHR
Marlborough Sounds, Maud [Te Hoiere] Island, on north east `corner' of peninsula	P26	86-	20-	1980	Among tauhinu - Olearia paniculata scrub, on sea cliff.		CHR
D'Urville Island, Port Hardy	P26			1941	Coastal scrub.cliffs		CHR
Seaview	P28	064	508	2001		4.4.5.2, 4.4.5.1	CHR, 62-67
Lower Awatere Valley	P28	00-	50-	1975			CHR
Wairau Valley	P28	70-	66-	1975			CHR
Lower Wairau Valley, near Branch [River]	P28	8--	5--	-			CHR
Picton Tuamarina Swamp	P28	8--	7--	1923	Margin of swamp.		CHR
south of Blenheim, Taylor Pass	P28	89-	52-	1967	Grassland.		CHR
Pukaka Valley	P28	9--	7--	1932			CHR
Wairau diversion, Marshlands	P28	9--	7--	1977			CHR
Tuamarina	P28	90-	66-	1914			CHR
Jordan Valley	P29	741	252	2000		4.4.4.5b	49,50
Isolated Hill	P29	915	231	2001		4.4.7b	149
Isolated Hill	P29	916	224	2001		4.4.4.2	144
Isolated Hill	P29	927	228	2001		4.4.7b	145
Isolated Hill	P29	927	229	2001		4.4.4.2, 4.4.7b	146-148
Lake Grassmere	P29	0--	4--	1937	Grassland.		CHR
Ward	P29	04-	30-	-	Limestone.		CHR
near mouth of Flaxbourne River	P29	07-	28-	1975	Limestone rubble, steep hillside.		CHR
Waima (Ure) River	P29	92-	24-	1967	Riverbank.		CHR
Waima River, north of Mount Benmore	P29	92-	24-	1973	Riverbank scrub.		CHR
George Stream	P30	722	999	2001		4.4.4.3a	154, 155
George Stream	P30	723	999	2001		4.4.4.3a	156
George Stream	P30	735	000	2001		4.4.4.2	157
George Stream	P30	737	001	2001		4.4.4.2	158
Wharekiri Stream.	P30	747	913	1985			CHR
Clarence River, 1.6 km above bridge	P30	7--	0--	1938	Rocky bluffs.		CHR

Wharf Valley	P30	7--	1--	1953			CHR
Lower Clarence River, Snowgrass Stream.	P30	72-	04-	1983			CHR
Blue Slip	P30	9--	1--	-			CHR
Woodside Creek	P30	9--	1--	1930			CHR
Kekerengu Valley	P30	91-	14-	1971	Riverbank.		CHR
Junction of Clinton River and Puhi Puhi River	P31	709	816	1977			CHR
Blue Duck Road	P31	743	865	2001		4.4.4.4	153
Blue Duck Road	P31	744	855	1975	Limestone bluffs above conifer/ hardwood forest of Blue Duck Reserve.		CHR

C. crassicaule							
Location	**Map**	**Grid reference E**	**N**	**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
Rangitata River	--			1956			CHR
Ben More St	--			-	1200ft		WELT
Mount Edward	E39	5--	2--	1937			CHR
Ben Lomond, Lake Wakatipu	E41	6--	6--	1921	var. racemosum, on shady rock, 3500 ft		WELT
Queenstown Hill	E41	6--	6--	1939			CHR
	E41	587	723	2001			DoC
Mt Rob Peak, Wanaka	F40	969	056	2001	var. racemosum		192
Remarkables skifield	F41	789	673	2001	var. racemosum		CHR, 195
Cardrona skifield	F41	922	847	2001	var. racemosum		CHR, 193
Lake County, Crown Range, 11.2 km south east of Arrowtown	F41	9--	7--	1962	In tussock grassland on steep slope.		CHR
Lake Wakatipu, Bayonet Peak	F42	7--	5--	1923			CHR
Remarkables, Wye Stream	F42	77-	54-	1995	Tussock grassland.		CHR
	G39	445	235	-			DoC
Mc Lays Ck, Lindis Pass	G39	476	213	2001		4.4.3.3b	256
North of Lindis Pass	G39	34-	31-	1994	On bluff to the north of pass.		CHR
Lindis Pass	G40	4--	1--	1937			CHR
Fairfax Spur	G41	151	648	2001		4.4.3.3b	200
Pisa Range	G41	153	865	-	820 m a.s.l.		DoC
Fairfax Spur	G41	159	648	2001		4.4.3.3b	201
Old Man Range	G42	131	450	2001		4.4.3.3b	221
Old Man Range	G42	133	452	2001		4.4.3.3b	222
Old Man Range, Syme Rd	G42	161	341	-	1300 m a.s.l.		DoC
Knobby Range	G43	281	280	2001		4.4.3.3b	220
Clutha River, west side of Roxburgh Lake, D. Hamilton's Property	G43			1971	Ungrazed semi-shaded knob.		CHR
South Canterbury, south of Braemar Station	H37	852	867	1970	Roadside.		CHR
Braemar Rd	H37	893	865	2001		4.4.3.3a	234
Liebig Range, Lower Jollie Valley, Mount Cook Station	H37	8--	0--	1966	Fescue tussock slopes.		CHR
East side Lake Pukaki, Tasman Downs Gates	H37	85-	85-	1975	Roadside, gone		CHR
Slopes east of L. Ohau	H38	619	581	2001		4.4.3.3c	100
near Lake Ohau, Greta Stream	H38	624	594	1969	In dense shade of beech forest remnant along stream.		CHR

Ben Ohau	H38	651	568	2001		4.4.3.3d	CHR, 102-104
Pukaki-Ohau Canal	H38	667	557	2001		4.4.3.3b	101
South Canterbury, Ohau River Terrace, site of canal	H38	678	556	1976	Stony soil.		CHR
Glen Lyon Rd	H38	685	574	2001		4.4.3.3a	126
Glen Lyon Rd	H38	685	574	2001		4.4.3.3a	127
Lake Ohau downs	H38	61-	51-	1994			CHR
South Canterbury, Lake Ohau 'Flats'	H38	---	---	1983			CHR
Ribbonwood	H39	569	436	2001		4.4.3.3b, 4.4.3.3a	135, 136
Wilderness Reserve, Bendhu	H39	608	390	1977	Amongst bog pine.		CHR
Cattle Ck	H39	703	232	2001		4.4.4.5c, 4.4.4.5b	129-131
Coal Ck	H39	840	321	2001		4.4.4.5c	247
North Otago, Omarama, Ribbonwood [Creek]	H39	5--	3--	1951			CHR
Mt St. Cuthbert	H39	7--	2--	-	2500 ft		WELT
St Bathans Range	H40	606	951	1979	Overhanging bank above wheel track.		CHR
Hawkdun, Home Hills	H40	673	933	2001		4.4.3.3d	209
Hawkdun, Home Hills	H40	685	941	2001		4.4.3.3c	210
	H40	593	964	2001			DoC
	H40	631	992	2001			DoC
	H40	638	016	2001			DoC
	H40	639	002	2001			DoC
	H40	612	991	2001			DoC
	H40	566	983	2001			DoC
	H40	564	958	2001			DoC
	H40	569	951	2001			DoC
	H40	575	958	2001			DoC
	H40	689	938	2001			DoC
Falls Dam	H41	650	876	2001		4.4.3.3b	199
Home Hills St	H41	682	898	2001		4.4.3.3c	211
Long Gully	H41	708	834	2001		4.4.3.3c	204
Little Mt Ida Rd	H41	735	747	2001		4.4.3.3b	225
Little Mt Ida Rd	H41	753	762	2001		4.4.3.3c	226
Long Gully	H41	771	853	2001		4.4.3.3d	202
Little Mt Ida	H41	784	793	2001		4.4.3.3a	227

southern flanks of the Ida Range, Deep Stream	H41	872	767	1997	Depleted Chionochloa rigida grassland; terraces above a deeply incised stream,		CHR
Naseby, Mount Ida	H41	7--	8--	1938	Lower slopes of mountain.		CHR, WELT
Naseby	H41	8--	7--	1975	Terrace near town.		CHR
Eweburn Creek, Maniototo Co.	H41	8--	7--	-	2000ft		WELT
Eweburn Race	H41	8--	7--	1905			WELT
	H41	662	861	2001			DoC
	H41	677	870	2001			DoC
	H41	884	870	2001			DoC
Poolburn Rd	H42	533	422	2001		4.4.3.2	205
Poolburn Rd	H42	534	408	2001		4.4.3.3b	206
Lynbrook St	H43	598	239	2001		4.4.3.3b	213
Old Dunstan Rd	H43	706	258	2001		4.4.3.3b	214
Cambrians Diggings, Vincent Co.	H44			-	1500 ft, lat 45 54, long 169 45		WELT
South Canterbury, Tekapo-Pukaki Highway	I37	009	829	1988			CHR
5km before Tekapo	I37	010	825	1994			CHR
Tekapo, roadside	I37	014	835	2001		4.4.3.3a	111
Tekapo, roadside	I37	016	837	2001		4.4.3.3a	112
Tekapo, Balmoral St., FR site	I37	020	830	2001		4.4.3.2	113
Lilybank Rd	I37	100	885	2001		4.4.3.2	237
4.3 km up Lilybank Rd	I37	102	891	1999			IG
Lilybank Rd	I37	142	976	2001		4.4.3.2	124
Round Hill	I37	194	055	2001		4.4.3.3c	119
Round Hill	I37	195	053	2001		4.4.3.3c	120
Round Hill	I37	195	051	2001		4.4.3.3c	121
Braemar Rd	I37	917	883	2001		4.4.3.3a	233
Lake Tekapo, 4.8 km up Lilybank Road	I37	10-	89-	1964	Rocks by shore.		CHR
Mackenzie Pass	I38	201	653	2001		4.4.3.2, 4.4.3.3c	139, 140
North of Mackenzie Pass	I38	1--	6--	1978	Grassland.		CHR
Hakataramea Pass	I38	12-	54-	1976			CHR
Mt Dalgety	I39	192	490	2001		4.4.3.3c	180
Mt Dalgety	I39	204	484	2001		4.4.3.2	176
Hakataramea Pass Rd, Rocky Point	I39	245	261	2001		4.4.3.1	174
Deep Stream	I40	001	149	2001		4.4.6.4	89-92
Between Hakataramea River and Waihao River, Meyers Pass area	I40	2--	1--	1967	Modified tussock grassland.		CHR
	I40	069	913	2001			DoC

South of Danseys Pass, Kyeburn Stream	I41	010	803	1986	Hanging over stream, almost horizontal.		CHR
Dansey's Pass Rd	I41	985	784	2001		4.4.3.3a	223
Dansey's Pass Rd	I41	992	795	2001		4.4.3.3d	224
Ben Lomond	I41	1--	8--	1921			CHR
near Kyeburn	I41	9--	7--	1943			CHR
Otago, South off Dansey's Pass, Kyeburn St	I41	9--	7--	1986	2500 ft, hanging over stream, almost horizontal, old plants, several stems 2cm diameter, about 1m long, much branched at apex		WELT
	I41	932	815	2001			DoC
	I41	901	698	2001			DoC
	I41	003	802	2001			DoC
	I41	013	815	2001			DoC
	I41	008	825	2001			DoC
Macraes Flat, Trig J	I43	053	241	2001		4.4.3.3a	DoC, 219
New Thorn Diggings, near Macraes	I43	0--	2--	-	1000 ft		WELT
Nenthorn Rd	I43	03-	23-	-			DoC
Tengawai River	J38	30-	67-	1995	Tussock grassland.		CHR
South Canterbury, Hunters Hills, Weaner Run	J39	378	285	1972	Ridge top.		CHR
Upper end of Pareora Gorge, south east of Dalziel Station	J39	3--	4--	1979	Growing in steep grassland in talus with Celmisia spectabilis; side of deep gorge.		CHR
Lake Lyndon Rd	K35	032	638	2001		4.4.3.4	CHR, 258
Porters Pass	K35	080	672	2001	Subalpine dracophyllum scrubland.	4.4.3.4	CHR, '76, 77
Porters Pass	K35	080	673	1968			CHR
Porters Pass	K35	081	673	2001		4.4.3.4	78
Porters Pass	K35	082	674	2001		4.4.3.4	79
Porters Pass	K35	083	675	2001		4.4.3.4	80
Fog Peak, Torlesse Range	K35	0--	6--	1948			WELT
Porters Pass	K35	08-	67-	1994	Terrace above stream bank - opean scrubland- stream on north side of Pass. Tussock Grassland		CHR
Canterbury Alps, Mount Taylor	K35	7--	4--	1874	Slopes of mountain.		CHR
Mid Canterbury, Mount Somers	K36	753	279	1972	On creek edge.		CHR
Mt Somers	K36	75-	33-	2001		4.4.3.4	245
Mount Somers, Woolshed Creek	K36	75-	31-	1982	Below scrub. In crevices of rock faces and ledges at creeksides (in vicinity of upper limits of Nothofagus solandri).		CHR

Mount Hutt, Waterfall Corner	K36	84-	39-	1985			CHR
Starvation Gully Mt Torlesse	L34	1--	7--	1891	2000-3000ft		WELT
Springfield, Thirteen Mile Bush, `Flaxy Spur'	L35	1--	6--	1961	2800 ft, abundant in community dominated by Phormium cookianum		CHR
Porters Pass	L35	10-	66-	1981			CHR
Puketeraki Range, Mount Whatno	M33	507	061	1973	> 3000 ft, fellfield		CHR
Puketeraki Range, Mt Whatno	M33	5--	0--	1973	>3000ft, fellfield		DoC
Mt Fyffe	O31	597	767	1995	near ridge on N side of mountain between hut and summit		DoC
Humpback, Kaikoura	O31	641	801	1999			DoC
Palmer Saddle	O31	3--	7--	-	P. A. Williams, Conway River headwaters below Mt Ross; believed to be extinct (S. Courtney, DoC Nelson)		DoC

C. curta							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Briar Ck, Ben Omar	H39	806	283	2001		4.4.6.4	DoC, 252
Ben Omar St	H39	809	281	-			DoC
Island next to Junction Is	H39	859	261	2001		4.4.6.2	169
Junction Is	H39	861	253	2001		4.4.6.3	170
Junction Is	H39	861	251	2001		4.4.3.2	171
Black Jacks Is	H39	876	265	2001		4.4.6.3	167
Black Jacks Is	H39	876	265	2001		4.4.6.3	168
North Otago, Omarama, Tara Hills Research Station	H39	62-	26-	1958			CHR
Otematata St	H40	859	174	-			DoC
Otematata St	H40	860	177	2001		4.4.6.2	185
Otematata St	H40	860	177	2001		4.4.6.2	186
Otematata St	H40	863	186	-			DoC
Otematata St	H40	864	186	2001		4.4.6.2	187
	H41	643	867	2001			DoC
Falls Dam	H41	651	881	1988	Rock outcrop below dam.		CHR
Falls Dam	H41	653	881	2001		4.4.6.4	207
Falls Dam	H41	653	881	2001		4.4.6.4	208
Maniototo Plain	H42	7--	5--	1909	dry ridges, various localities there (Sowburn).		WELT
Eweburn, Maniototo Co.	H42	8--	5--	1908			WELT, CHR
Mt John	I37	062	880	-			DoC
Mt John	I37	065	884	2001		4.4.6.3	117
Mt John	I37	066	885	2001		4.4.6.3	116
Mt John	I37	067	887	-			DoC
Mt John	I37	068	887	2001		4.4.6.3	115
Sawdon St	I38	101	799	2001		4.4.6.3	164
Sawdon St	I38	101	798	-			DoC
Sawdon St	I38	102	800	-			DoC
Sawdon St	I38	103	799	-			DoC
Sawdon St	I38	103	800	2001		4.4.6.3	162, 163
Glenrock St	I38	129	709	2001			DoC
Mackenzie Pass	I38	160	654	2001		4.4.3.2	160, 161
Mackenzie Pass	I38	161	654	2001		4.4.3.2	159
Deep Stream	I40	001	149	2001		4.4.6.4	58, 91, 92

Awahokomo Stream	I40	029	081	2001	300 m,on alluvium amongst grey scrub bordering river.		DoC, CHR, AK
Lake Waitaki roadside	I40	031	108	1993	Roadside terrace.		CHR
Lake Waitaki roadside	I40	033	108	-			DoC
Lake Aviemore roadside	I40	905	177	1994	280 m, roadside bank, browsed, spray damage, few seedlings.		AK
Lake Aviemore, roadside	I40	914	175	-			DoC
Lake Aviemore, roadside	I40	919	173	2000		4.4.6.2	34, 86
North Otago, nearest major locality Otematata, Waitaki Valley, below Otematata	I40	928	169	1994	Stony ground among dryland grasses on toe slope of hillside. On ungrazed ground in 15 m wide strip between edge of high road cutting and fenceline.		RARE
Waitaki valley, below Otematata	I40	928	168	1994	Stony ground on toe slope of hillside.		CHR
Lake Aviemore, roadside	I40	932	168	2001		4.4.6.2	87, 88
Lake Aviemore, roadside	I40	939	161	2001		4.4.6.3	95
North Otago, Lake Aviemore	I40	945	156	1980	Dry hillside at top of road cutting.		CHR
Lake Aviemore	I40	950	149	1996	Shingle at roadside - old river terrace.		CHR
Lake Aviemore, roadside	I40	981	175	-			DoC
Deep Stream	I40	999	147	2000		4.4.6.4	57
Deep Stream	I40	999	148	2001		4.4.6.4	DoC, 93
Hills near Kurow	I40	0--	0--	1931			CHR
Waitaki Valley, below Dam, south bank	I40	0--	0--	1975	Steep rocky bank, ledge.		CHR
Lake Waitaki roadside	I40	0--	1--	1983			CHR
Lake Waitaki	I40	00-	10-	1976	Roadside cuttings by stockyards.		CHR
	I40	05-	09-	-	On roadside.		CHR
	I40	05-	09-	-	On roadside.		CHR
Duntroon	I40	2--	9--	-	flood plain of Waitaki River; extinct.		WELT, CHR
Lake Aviemore	I40	91-	13-	1976			CHR
	J41	33-	89-	-			CHR
Maheno nr Oamaru	J42	42	57	-	semierect plant 21/2-3 ft high, little branched at the base but freely branched towards the tops, among grass and sparse manuka, mostly on dry slopes; extinct.		WELT
Terraces on coast sth of Oamaru towards Kakanui Mouth	J42	48	55	-	extinct.		WELT
Kakanui River Mouth	J42	4--	5--	-	extinct.		WELT

C. hollowayi							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Awahokomo	I40	022	085	2001		4.4.6.1	35, 84, 85
North Otago, nearest major locality Kurow, Waitaki Valley, Awahokomo Creek, south of Lake Waitaki	I40	023	083	1992	Spur on top of limestone outcrop on hillside.		RARE
Awahokomo	I40	023	085	2001	Base of limestone cliffs in short tussock grassland.	4.4.6.1	AK, CHR, 81, 82
Awahokomo	I40	023	086	1994	480 m, limestone bluff top, scale insects.		AK
Waitaki Valley, Gards Road	I40	12-	95-	1976			CHR
Waitaki Valley, Gards Road	I40	145	973	1983	Limestone Cliff.		CHR
Gards Road, Limestone Outcrop	I40	148	973	1995	Edge of limestone cliff.		CHR
Gards Rd	I40	149	972	2001			96
Waitaki Valley, above Maori petroglyphs	I40	237	933	2001	On limestone.	4.4.6.1	CHR, 172, 173
Duntroon.	I40	26-	91-	1983			CHR
North Otago, Waitaki Valley, near Duntroon, foot of Mt St Mary	I40	---	---	1939	Sandstone.		CHR
foothills of Saint Mary's Range (Mt St Mary)	I40	---	---	0			AK
	I40	028	097	2001			Brian Molloy

C. juncea							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
shores of Lake Manapouri, below accomodation house	C43	8--	0--	1909	extinct.		AK
Fiordland, Shores of Lake Manapouri, near the jetty	C43	8--	0--	1951	Edges of banks near stony shores; extinct.		CHR, WELT
Clinton Valley, Darran ED	D41			-			AK
Lake Wanaka, Makarora	F39	076	490	-	Creek margins.		CHR, WELT
Makarora River	F39	---		-	margins of Makarora River		AK
South Westland, nearest major locality Fox Glacier, Fox River, approximately 500m downstream of State Highway 6 bridge	H35	676	435	1999	Upstream end of stable riverbed island. Consolidated boulder pile, with short tutu, mosses and Gunnera species predominating with grass and Raoulia species around plants of Carmichaelia juncea.	4.4.1.2	RARE, 7
Fox River	H35	681	434	1999	In silt, in open river flat above normal flood level.	4.4.1.2, 4.4.1.1	CHR, 5, 6
South Westland, nearest major locality Fox Glacier, Fox River, approximately 1 km upstream of State Highway 6 bridge	H35	688	438	1998	Grassed, stable bank of island.		RARE
Waiho River	H35	792	560	1999		4.4.1.1	10, 11, 12
Waiho River	H35	797	552	1999		4.4.1.2	1
Waiho River	H35	800	555	1999		4.4.1.1	13
Waiho River	H35	800	557	1999		4.4.1.1	9
Waiho River	H35	805	555	1999		4.4.1.1	8
Waiho River	H35	807	552	1999		4.4.1.2	14
Waiho River	H35	814	547	1999		4.4.1.1	2
South Westland, Cook River Flats, near trig JD	H35	59-	44-	1967	Colonising flood-plain gravels.		CHR
Cook River	H35	64-	40-	1982			CHR
Waiho River	H35	70-	60-	2001			DoC
Waiho River, 1 mile below terminal face of Franz Joseph Glacier	H35	80-	49-	1962	River shingle.		CHR
Waiho River	H35	---	---	1924	very abundant all over riverbed, also other rivers of the district (A. Wall).		WELT
Welcome Flats	H36	647	257	1999		4.4.1.2	19
Welcome Flats	H36	647	258	1999		4.4.1.2	18

South Westland, nearest major locality Fox Glacier, Upper Welcome Flat Copland Valley	H36	660	256	1998	Adjacent to old river channel, on the edge of established vegetation including scabweed, Gunnera species.		RARE
Welcome Flats	H36	662	254	1999		4.4.1.2	17
Welcome Flats	H36	663	255	1999		4.4.1.2	16
Welcome Flats	H36	663	256	1999		4.4.1.2	4
Welcome Flats	H36	667	254	1999		4.4.1.2	3, 15
Hooker Valley	H36	7--	1--	1912			WELT
Maniototo	H41/ H42	7--	5--	-			AK
Wanganui River	I34	---	---	1946	Sandy river flat.		CHR
Lake Lyndon	K35	0--	6--	1896	2600 ft, just where the tussock merges into mud of lake, edge of tussock adjoining shore of Lake Lyndon, in clayey ground, facing south, but exposed to full sunshine; extinct.		WELT, AK
Lake Marymere	L34	16-	87-	1938	Edges of lake, amongst stones; extinct.		CHR
Near Farewell Spit, south west of Whahariki, Green Hills Stream	M24	8--	7--	1905	A. P. Druce, 50 ft vertical conglomerate cliff facing S; 8 plants seen, could be many more on 200 ft cliff.		
Near Farewell Spit, south west of Whahariki, Green Hills Stream	M24	807	777	2000	On conglomerate. Coastal rocks at east end of beach. Very exposed, 8 plants.	4.4.2	CHR, 21
Northwest coast, Sandhill Creek	M25	586	592	1975	Seacliff top, mat vegetation; extinct.		CHR
West Wanganui Inlet	M25	654	651	1924			CHR
Westhaven, NW Nelson	M25	--	---	1935	sandstone ledges on innermost island.		DoC
Sandhills Ck, NW Nelson	M25	5--	5--	1982	10 ft; extinct.		DoC
(Hutt Valley, Pinehaven)	M25	58-	58-	1982			CHR
West Wanganui Inlet	M25	6--	6--	1947			CHR
(Dunedin, garden of G Simpson)	M25	6--	6--	1935	Sandstone ledges on innermost island of three.		CHR
West Wanganui Inlet	M25	6--	6--	1918	sandstone island in centre of West Wanganui Inlet.		WELT
Bank of Clarence River between Valleys leading to Jack's and Jollies Passes	N31	9--	6--	1917			WELT
Upcot Saddle	O30	5--	1--	1916			WELT
Matukituki				-	river bed.		WELT
Nguroa Bay				-			DoC
					Amongst stones on shore subject to immersion at very high lake level.		CHR

C. kirkii							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
	F40	001	907	1999	Kate Wardle		DoC
Deep Ck	F40	003	907	2001		4.4.4.5a	194
Central Otago, Deep Creek, Cardrona Valley	F40	006	901	1985	Scrub at stream.		CHR, RARE
Nearest major locality Lindis Pass, about 19.3 km south of Lindis Pass	G40	266	036	1970			RARE, CHR
Central Otago, Big Spur Creek (trib. of Cluden Stream)	G40	389	928	1985	Scrub at stream.		CHR
Nearest major locality Lindis Valley, in the northwest Dunstan Mountains, along mid-portion and tributaries of Cluden Stream	G40	397	933	1984	Altitude 502-670m. Along streamside sprawling over shrub species such as Discaria toumatau, Coprosma propinqua, Olearia odorata, Aristotelia fruticosa, Hebe salifolia (in order of dominance), within 3m of stream.		RARE
Nearest major locality Lindis Valley, in northwest Dunstan Mountains, along the mid-portion and tributaries of Cluden Stream	G40	397	947	1984	Altitude 502-670m. Along streamside sprawling over shrub species such as Discaria toumatau, Coprosma propinqua, Olearia odorata, Aristotelia fruticosa, Hebe salifolia (in order of dominancea), within 3m of stream.		RARE
Central Otago, (unnamed) tributary of Cluden Stream	G40	399	929	1985	Scrub at streamside.		CHR
Tributary of Cluden St	G40	400	927	2001	Altitude 502-670m. Along streamside sprawling over shrub species such as Discaria toumatau, Coprosma propinqua, Olearia odorata, Aristotelia fruticosa, Hebe salifolia (in order of dominance), within 3m of stream.	4.4.4.5a	AK, RARE, 189, 190, 191
Nearest major locality Lindis Valley, in northwest Dunstan Mountains, along the mid-portion and tributaries of Cluden Stream	G40	433	973	1984	Altitude 502-670m. Along streamside sprawling over shrub species such as Discaria toumatau, Coprosma propinqua, Olearia odorata, Aristotelia fruticosa, Hebe salifolia (in order of dominance), within 3m of stream.		RARE

Nearest major locality Lindis Valley, in northwest Dunstan Mountains, along the mid-portion and tributaries of Cluden Stream	G40	434	972	1984	Altitude 502-670m. Along streamside sprawling over shrub species such as Discaria toumatau, Coprosma propinqua, Olearia odorata, Aristotelia fruticosa, Hebe salifolia (in order of dominance), within 3m of stream.		RARE
Nearest major locality Cox's Downs, Mount Cook Station, Cox's Downs	H37	825	997	1970	Single plant in creek bed of plantation.		RARE
South of Mount Cook station, Lake Pukaki	H37	832	986	1970	Creek bed in plantation, Pinus.		CHR
Nearest major locality Cox's Downs, Tasman River at head of Lake Pukaki, Cox's Downs	H37	840	999	-	In shrubs along stream edge of plantation; extinct.		RARE
Nearest major locality Twizel, Ohau River on island and adjacent river bank	H38	688	552	-	extinct.		RARE
Nearest major locality Lake Pukaki, Lake Pukaki	H38	803	686	-	Among scrub; extinct.		RARE
Ohau River	H38	68-	54-	-	extinct.		CHR
Nearest major locality Twizel, Ohau River bed, upstream and downstream from Lake Ruataniwha	H38	77-	53-	-	extinct.		RARE
Lake Pukaki, South Canterbury, Hermitage Rd, 1/2 - 1 mile from lake. Tekapo ecological district	H38	80-	65-	-	In Coprosma propinqua scrub; extinct		RARE
Hermitage road, .8-1.6 km from Lake Pukaki	H38	---	---	-	Coprosma propinqua scrub; extinct.		CHR
Lake Pukaki	H38	---	---	1942	Among scrub; extinct.		CHR
Ohau River bed, upstream from Lake Ruataniwha	H38	7--	5--	-	Riverbed; extinct.		CHR
Cattle Ck	H39	686	224	2001		4.4.4.4	133
Cattle Ck	H39	692	219	2001		4.4.4.5a	134
Nearest major locality Omarama, south of Omarama, Headwaters of Cattle Creek	H39	693	216	1996	Mixed Grey Scrub (Coprosma sp., Matagouri, Corokia cotoneaster, Porcupine shrub, Hebe sp., Parsonsia capsularis, Rubus sp., Muehlenbeckia complexa, some Myrsine australis).		RARE
Nearest major locality Omarama, south of Omarama, Mount Saint Cuthbert	H39	695	214	1996	Mixed Grey Scrub (Coprosma sp., Matagouri, Corokia cotoneaster, Porcupine shrub, Hebe sp., Parsonsia capsularis, Rubus sp., Muehlenbeckia complexa, some Myrsine australis).		RARE

Mackenzie Country, Omarama, St Cuthbert Range, head of Cattle Creek	H39	702	230	1986	Boulder field on steep slope (stable). South aspect.		CHR
Cattle Ck	H39	703	232	2001		4.4.4.5b	128, 130
Benmore Range, Silver Creek	H39	755	347	1984			RARE
Benmore Range, Silver Creek	H39	756	349	1983			CHR
Benmore Range, Brier Creek	H39	802	265	1984			RARE
Benmore Range, Brier Creek	H39	802	274	1984			RARE
Briar Ck, Ben Omar	H39	807	284	2001		4.4.4.5c	253
Briar Ck, Ben Omar	H39	808	284	2001		4.4.4.5c	254
Briar Ck, Ben Omar	H39	808	285	2001		4.4.4.5c	255
Benmore Range, Poplars Bridge Gully	H39	811	265	1984			RARE
	H39	811	266	2000			DoC
Nearest major locality Otematata, Benmore Range	H39	811	287	1982	Lianoid shrub climbing up through woodland Hall's totara on hillside.		RARE, CHR
Benmore Range, Glencairn	H39	816	476	1984			RARE
Benmore Range, Glencairn	H39	816	485	1984			RARE
Poplars Bridge Gully	H39	817	269	-			CHR
Benmore Range, Coprosma Creek	H39	820	266	1984			RARE
Totara Peak	H39	82-	33-	-	extinct.		DoC
Benmore Range, Scrubby Creek	H39	826	430	1984			RARE
Benmore Range, Black Stilt Gully	H39	826	448	1984			RARE
Nearest major locality Twizel, Lower Ohau River, Benmore, Cairn Gully, near head of lake	H39	828	487	1983	Near lower end of willows.		RARE
Benmore Range, southern end	H39	834	281	1983			CHR
Benmore Range, Scrubby Creek - left branch	H39	835	430	1984			RARE
Benmore Range, Triangle Scrub Creek	H39	835	439	1984			RARE
Benmore Range, Falstone Creek	H39	836	403	1984			RARE
Benmore Range, Shepherds Creek	H39	837	339	1984			RARE
Benmore Range, Shepherds Creek	H39	837	348	1984			RARE
Benmore Range, Swampy Creek	H39	838	275	1984			RARE
Coal Ck	H39	840	321	2001		4.4.4.5c	248
Scrubby Ck	H39	841	437	2000		4.4.4.5a	56
Coal Ck	H39	842	321	2001		4.4.4.5c	249
Camp Ck	H39	843	431	2001		4.4.4.5a	165
Coal Ck	H39	846	319	2001		4.4.4.5c	251
Benmore Range, Shepherds Creek	H39	846	348	1984			RARE
Benmore Range, Turnagain Creek	H39	848	285	1984			RARE

Benmore Range, Snake Creek	H39	853	304	1984			RARE
Benmore Range, Snake Creek	H39	855	287	1984			RARE
Benmore Range, Coal Creek	H39	856	321	1984			RARE
Benmore Range, Coal Creek	H39	864	339	1984			RARE
Benmore Range, Lone Tree Creek	H39	864	385	1984			RARE
Benmore Range, Coal Creek	H39	865	330	1984			RARE
Lone Tree Ck	H39	865	389	2001	Open grassland, no shrub support.	4.4.4.5a	166, CHR
Benmore Range, Willow Creek	H39	868	374	1984			RARE, CHR
Benmore Range, Totara Creek	H39	77-	30-	1984			RARE, CHR
Peak Valley Creek	H39	82-	28-	1983			CHR
Totara Peak	H39	82-	33-	1979	In Hall's totara stand.		CHR
Camp Creek	H39	82-	42-	1983			CHR
Benmore Range, Swampy Creek	H39	83-	27-	1984			RARE
Benmore Range, Peak Valley Creek	H39	83-	28-	1984			RARE
Nearest major locality Ben Omar, Totara Peak	H39	83-	33-	1979	In halls totara stand, shrublike form amongst other shrubs.		RARE
Benmore Range, Camp Creek	H39	83-	42-	1984			RARE
Black Stilt Gully	H39	83-	45-	1983			CHR
Benmore Range, Black Stilt Gully	H39	83-	46-	1984			RARE
Benmore Range, Shepherds Creek.	H39	84-	34-	1983			CHR
Camp Creek	H39	85-	42-	1983			CHR
Benmore Range, Snake Creek, Upper Valley	H39	---	---	1983			CHR
Benmore Range, Turnagain Creek	H39	---	---	1983			CHR
Blackstone Hill	H41	566	743	2001		4.4.4.4	197, 198
Nature Gully	H41	63-	66-	1999			DoC
Gimmerburn, Otago	H42	569	751	-	extinct.		AK
Central Otago, Nearest major locality Gimmerburn, Maniototo Basin, Gimmerburn, where western irrigation race for Maniototo enters siphon to cross Wether Burn	H42	735	565	-	extinct.		RARE, CHR
Sowburn, Maniototo	H42	---	---	1892			WELT
Lynbrook St	H43	591	245	2001		4.4.4.5a	DoC, 212
Nearest major locality Wharekuri, near Lake Aviemore, northeast side above dam	I40	000	148	-	extinct.		RARE
Stoney Ck	I40	992	165	2001		4.4.4.6	DoC, RARE, 94
Stoney Ck	I40	993	169	2000			DoC
Stoney Ck	I40	992	166	2000			DoC
Deep Stream	I40	000	148	-	Peter Johnson; extinct		DoC

Nearest major locality Kurow	I40	993	166	1991	Rocky gully with mixed Coprosma propinqua and Discaria toumatou scrub.		RARE
Nearest major locality Macraes, Macraes Flat, Murphys Creek	I42	125	322	1991	Single plant in bluff in bottom of gully, among sub-alpine Chionochloa rigida grassland.		CHR, RARE
Murphy's Ck	I42	125	323	2001		4.4.4.5b	218
Nearest major locality Macraes Flat, southeast of Macraes Flat, Murphys Creek headwaters, below Trig 'D' next to Golden Bar Road	I42	126	323	1995	Rock overhang on toeslope in snow tussock grassland.		RARE
near Waihemo, Dunback	I42	195	409	2001	Steep dry bank above stream.	4.4.4.6	CHR, 229
Waihemo	I42	196	408	2001		4.4.4.6	230
Sheepwash Ck	I43	924	175	2001		4.4.4.5b	217
Nearest major locality Middlemarch, Middlemarch area, Sheepwash Creek tributary, south of Slip Hill, next to Moonlight Road, at west end of a deeply incised section of creek	I43	926	174	2001	In shrubland of Coprosma propinqua, Discaria toumatou, Carmichaelia virgata, and Muehlenbeckia complexa.	4.4.4.5a	RARE, 216
Taieri Ridge, Sheepwash Creek	I43	92-	18-	1995	Scrub.		CHR
Kowhai Ridge, Te Moana Gorge	J37	512	828	2001		4.4.4.5a	183
River bank south of Otepopo Tunnel, Waitaki Co.	J42	3--	5--	-	I had many specimen from this station, they are here no longer'; extinct		WELT
Otepopo	J42	3--	5--	-	slopes above river; extinct		AK
North Otago, slopes above Otepopo River, between the road and railway tunnel	J42	3--	5--	-	River terraces; extinct.		CHR, RARE
Nearest major locality Windwhistle, Rakaia Gorge near Windwhistle, on island	K35	0--	1--	-	extinct.		RARE
Nearest major locality Arthur's Pass, Poulter River	L34	153	899	1984	Among scrub on river terrace.		RARE
Nearest major locality Mount White, Poulter River, east or true left side of river at mouth of gorge, and 0.5km downstream of road bridge	L34	210	953	1993	Terrace facing south. Sandy sites.		RARE
Poulter River	L34	211	952	2000		4.4.4.5a	CHR, AK, 51, 52, 53
0.5km south of Poulter Bridge, terrace face	L34	211	953	1989	Open scrub on terrace face, facing south.		CHR
Nearest major locality Oxford, Oxford, View Hill	L35	322	646	1968	In swampy forest on flat ground across the road from reserve.		RARE
west of Coopers Creek	L35	350	685	1978	Forest on poorly drained plain.		CHR
View Hill	L35	350	686	2000		4.4.4.5a	28
View Hill	L35	352	682	1999	recently fenced forest remnant		IG

Rampaddock Rd, Viewhill	L35	350	687	1995	trailing through Cop obconica in understorey, 300 m		AK
Rampaddock Rd, Viewhill	L35	352	682	1999			DoC
Oxford, View Hill Scenic Reserve	L35	32-	65-	1968	Swamp forest on flat across road from reserve.		CHR
Coopers Creek (near Viewhill)	L35	34-	67-	1981			CHR
Viewhill, Rampaddock Road	L35	35-	67-	1979			CHR
Nearest major locality Christchurch, New Brighton	M35	875	436	1918	Amongst Coprosma propinqua bush in tidal swamp.		RARE, CHR
New Brighton	M35	8--	4--	-	climbing over Cop prop in Phormium tenax swamp; in swamp under willows; tidal swamp		AK
New Brighton, Christchurch	M35			1899	growing in slightly swampy ground and climbing over Coprosma propinqua in shade of Phormium, now nearly all destroyed by fire, neighbourhood of New Brighton at foot of sanddunes		WELT
Banks of Avon River, New Brighton	M35			-			WELT
Port Levy, Beacon Bay	N36	987	330	1999			CHR, DoC
Port Levy, Akiraha Bay	N36	993	327	1999	Altitude 5-45m. Site is highly modified scattered shrubs along stream which has trickles of water only.		CHR, RARE, DoC
Yeo Stream	O30	325	975	1997	browsed, through Coprosma and matagouri near stream, 960 m		AK
Tone Valley	O30	429	999	2000		4.4.4.1	26
Tone Valley	O30	441	989	2000		4.4.4.4	24
upper Tone [River], west bank.	O30	443	001	1984	Scrub on stream bank.		CHR
Tone Valley	O30	443	992	2000		4.4.4.5a	25
Tone Valley	O30	450	011	2000		4.4.4.3a	27
(Hutt Valley, Pinehaven)	O30	56-	13-	1990			CHR
Mowatts Lookout				1916			WELT

C. muritai							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Clifford Bay, Seaview	P28	064	505	1994	80 m a.s.l.		AK
Clifford Bay, Seaview	P28	064	508	2001		4.4.5.1	64, 66-68
Te Parinui o Whitu	P28	059	601	2001		4.4.5.3	DoC, 259

C. stevensonii							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Clarence Bridge	---			-			WELT
Wairau Valley	---			-			WELT
Lower Clarence	---			1923			CHR
Tummil River	O29	448	651	1991	320 m,one 3m tall tree at edge of deep gorge in wet seepage amongst kowhai and hawthorn; extinct.		AK, CHR
Avon Valley	O29	579	384	2000	planted; extinct.		
Avon Valley, 1 km down valley from Malvern Hills Station	O29	5--	3--	1977	Beside river with Kanuka three quarters broadleaf scrub; extinct.		CHR
Avondale	O29	6--	4--	-	extinct.		CHR
Upcot	O30	5--	1--	-			DoC
Camden St	O29	6--	2--	-			DoC
Mid and Upper Jordan River	P29	7--	2--	1981			CHR
Awatere Valley, Jordan River	P29	72-	27-	1967	Stream bank (alluvial soil).		CHR
George Pass	P30	719	998	1999		4.4.4.3a	45
George Stream	P30	72-	99-	-	914 m.		AK
George Stream	P30	723	999	2001		4.4.4.3a	156
Miller Stream Catchment	P30	74-	97-	1981	At riverside.		CHR
Mt Alexander	P30	754	905	2001		4.4.4.3b	CHR, 48, 150, 151
Mt Alexander	P30	755	905	2001		4.4.4.3b	152
Mount Alexander	P30	756	904	1985			CHR
Totara Saddle, Gibson Stream (Clarence R)	P30	7--	0--	-			DoC
Snowgrass Stream (south of the big bend of the Clarence)	P30	7--	0--	-			AK
Clarence River, Snowgrass Stream	P30	7--	0--	1982			CHR
Clarence (Waiautoa) Bridge	P30	7--	0--	1910			AK
Miller Stream, right branch	P30	7--	9--	1984			CHR
Lower Clarence Valley, head of Miller Stream	P30	7--	9--	1981			CHR
Miller Stream, left branch	P30	7--	9--	1984			CHR
Wharekiri	P30	7--	9--	-			DoC
Clarence Valley	P31	86-	93-	1953			CHR
Mt Aston? Waihopai Valley					grub in nearly every pod		WELT
Upper Avon Valley, Malvern stream				1981			CHR
Flaxton				1923			CHR

C. vexillata							
Location	**Map**	**Grid reference**		**Latest year**	**Notes in historical records**	**Community (chapter 4)**	**Source**
		E	**N**				
Mount Edward	E39	5--	2--	1938			CHR
Central Otago, Cromwell, Kawarau River, Mount Difficulty	F41	0--	6--	1987	Gravel patches (schistose) on open broad ridge crest.		CHR
Cromwell, Kawarau River, Mount Difficulty	F41	007	653	1986	Acaena and Raoulia cushions, and very sparse tussock.		CHR
Mt Difficulty	F41	010	656	2001		4.4.3.3a	196
west slopes of Wether Range, near McLays Creek	G39	4--	2--	1960	Danthonia rigida grassland.		CHR
Lindis Pass	G40	4--	1--	1939	Tussock grassland on hills above Pass.		CHR
Lindis Pass	G40	43-	19-	1975			CHR
Lindis Pass	G40	434	190	2001		4.4.3.3a	188
Liebig Range, Mount Cook Station, Mount Burnett	H37	8--	0--	1964			CHR
Lake Pukaki, Tasman Downs, Boltons Gully	H37	847	824	1970	North west aspect, very exposed bare loess.		CHR
Lake Pukaki, Tasman Downs, Boltons Gully	H37	856	824	1970	At top of road cutting.		CHR
Boltons Gully	H37	860	829	2001		4.4.3.2, 4.4.3.1	105, 106
Lake Pukaki, Boltons Gully	H37	865	824	1975			CHR
Boltons Gully	H37	866	829	2001		4.4.3.2	DoC, 107
Boltons Gully	H37	866	830	2001		4.4.3.2	DoC, 108
Pukaki-Ohau Canal	H38	674	558	2001		4.4.3.1	DoC, 99
Ohau-Pukaki Canal	H38	674	559	1994	520 m,modified tussock grassland		AK, CHR
Ohau River	H38	678	556	1976	River terrace, site of canal. Silty soil.		CHR
Pukaki-Ohau Canal	H38	678	560	2000		4.4.3.1	42
Pukaki-Ohau Canal	H38	681	562	2000		4.4.3.1	43
Pukaki-Ohau Canal	H38	687	565	2000		4.4.3.1	DoC, 44
Mackenzie Basin, power line ISL TWL210	H38	8--	5--	1976			CHR
Ribbonwood	H39	568	435	2001		4.4.3.3b	137
Coal Ck	H39	842	320	2001		4.4.3.3b	250
Snake Creek	H39	851	311	2000			DoC
Snake Creek	H39	856	299	2000			DoC
Upper Waitaki Valley, Otematata	H40	8--	1--	-	Stony roadsides.		CHR
North Otago, Waitaki Valley, Otematata Station	H40	8--	1--	1939	Stony ground in front of Otematata Station.		CHR
Ida valley	H41	---	---	-	1800 ft		WELT

St Bathan's	H41	50-	80-	1892	2000ft		WELT
Little Mt Ida	H41	774	792	2001	monroi?	4.4.3.3a	228
Long Gully	H41	775	852	2001	monroi?	4.4.3.3d	203
Naseby	H41	8--	7--	1910	Terrace right of the road near the town.		CHR
Naseby, Mount Ida, lower part of Tourist Spur	H41	8--	7--	1970	Fine scree spur.		CHR
Naseby	H41	80-	70-	1889			WELT
Mt Ida	H41	80-	82-	1975			CHR
Maniototo Plain	H41/ H42	---	---	-			WELT
Beattie's Covenant	H42	717	395	2001		4.4.3.1	215
	H42	87-	54-	-			CHR
Round Hill	I37	193	048	2001		4.4.3.2	DoC, 122
Round Hill	I37	194	055	2001		4.4.3.2	DoC, 118
Round Hill	I37	199	061	2001		4.4.3.3a	DoC, 123
Tekapo Military Area	I37	014	960	2000		4.4.3.3a	DoC, 37
Tekapo Military Area	I37	014	966	2000		4.4.3.2	DoC, 36
Tekapo Military Area	I37	015	964	2000		4.4.3.2	DoC, 38
near Tekapo, Mount John Station	I37	016	961	1977	Dry knoll in Festuca novae-zelandiae grassland.		CHR
Tekapo, Balmoral St., FR site	I37	043	827	2001		4.4.3.2	39, 40, 41, 110
South Canterbury, Lake Tekapo, Mount John, DSIR Trial site	I37	058	887	1982	Near Festuca among Hieracium, flat area.		CHR
Mt John	I37	068	887	2001		4.4.3.3b	DoC, 114
Mt John	I37	071	911	2000			DoC
In Tekapo, 5km up Lilybank Road	I37	09-	87-	1995	Hieracium modified grassland.		CHR
Lake Tekapo, Round Hill	I37	19-	05-	1993	Moraine, tussock grassland.		CHR
South Canterbury, Two Thumb Range, near Round Hill	I37	190	049	1985	Moraine.		CHR
South Canterbury, Mackenzie Pass	I38	197	647	1970	Eroded face, north aspect, 600-700 metres.		CHR
Mackenzie Pass	I38	199	654	2001		4.4.3.3a	DoC, 138
Mackenzie Pass	I38	201	653	2001		4.4.3.2	DoC, 141
Irishman Ck	I38	958	777	2000			DoC
Irishmans Creek, Braemar Road.	I38	97-	78-	1975	Edge of loess bank.		CHR
Irishman Ck	I38	973	782	2001		4.4.3.1	DoC, 109
Irishman Ck	I38	984	788	2001		4.4.3.2	DoC, 125
Mt Dalgety	I39	192	487	2001		4.4.3.3c	179
Kurow	I40	0--	0--	1919	old river bed		WELT
Awakino	I40	066	077	2001		4.4.3.2	97

North Otago, near Kurow, between Awakino and Little Awakino River	I40	066	078	1981	Rocky sparse grassland.		CHR
Lake Waitaki	I40	0--	1--	1983	Roadside.		CHR
St Mary Range, Mount St Mary	I40	9--	1--	1975			CHR
Waitaki Dam	I40	9--	1--	-	Shingly ground near Dam.		CHR
Mount St Mary	I40	---	---	1938	In grassland 760-1065 metres.		CHR
Awatere Valley, Dumgree	P28	94-	51-	2001	On river terrace above plantations.		CHR
Nina Brook	P29	922	494	2001			DoC

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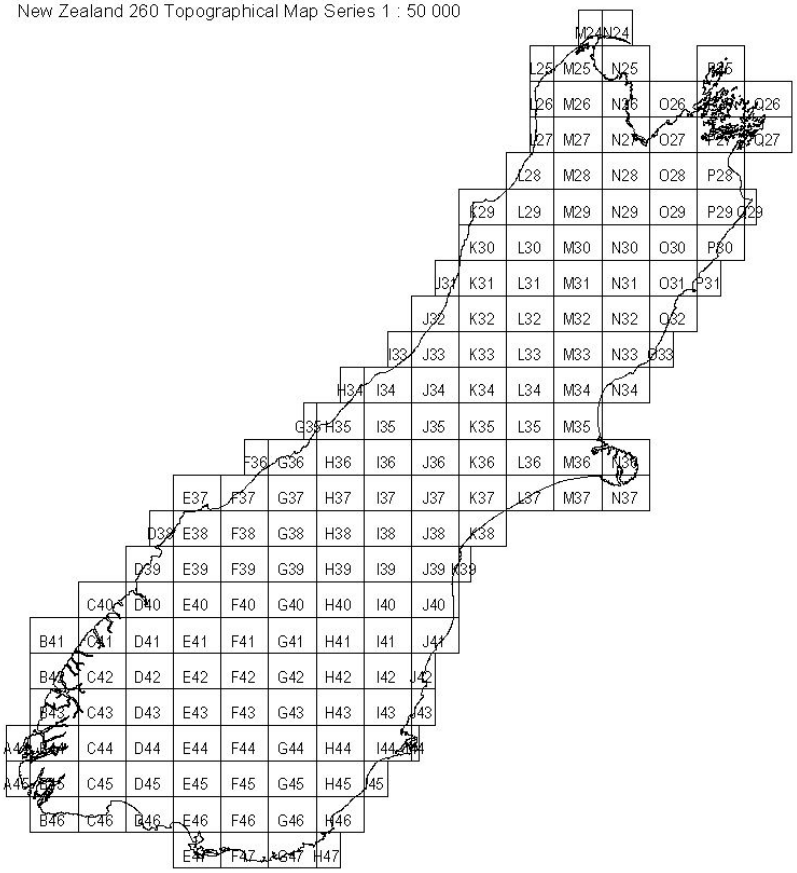

Appendix 2

Overview over vegetation types and plant communities in habitats of *Carmichaelia* (chapter 4).

4.4.1 Pioneer vegetation

4.4.1.1 [*Raoulia hookeri*] sand- or gravelfield

4.4.1.2 [*Raoulia hookeri*] – [*Holcus lanatus*] grassland

4.4.2 Cliff face vegetation, Northwest Nelson

4.4.3 Grassland vegetation

4.4.3.1 [*Agrostis capillaris*] – [*Hieracium pilosella*] sandfield

4.4.3.2 *Hieracium pilosella* herbfield

4.4.3.3 (*Chionochloa* spp.) – (*Hieracium pilosella*) tussock grassland

- a Type with *Hieracium pilosella*
- b Type with *Acaena caesiiglauca*
- c Type with *Brachyglottis bellidioides*
- d Type with *Gaultheria crassa*

4.4.3.4 [*Gaultheria crassa*] – [*Chionochloa* spp.] tussock-shrubland

4.4.4 Scrub and shrubland vegetation

4.4.4.1 (*Hebe traversii*) shrubland

4.4.4.2 [*Leptospermum scoparium*] /(*Coriaria arborea*) shrubland

4.4.4.3 [*Podocarpus hallii*] shrubland

- a Type with *Phyllocladus alpinus*
- b Type with *Polystichum vestitum*

4.4.4.4 *Discaria toumatou* grass-shrubland

4.4.4.5 *Coprosma propinqua* – [*Aristotelia fruticosa*] shrubland

- a Type with *Polystichum vestitum*
- b Type with *Poa cita*
- c Type with *Podocarpus hallii*

4.4.4.6 *Coprosma propinqua* – [*Sophora microphylla*] scrub

4.4.5 Coastal grass- and shrubland vegetation

4.4.5.1 *Olearia paniculata* shrubland

4.4.5.2 (*Dactylis glomerata*) – (*Bromus willdenowii*) grassland

4.4.5.3 *Rytidosperma racemosum* grassland

4.4.6 Ruderal and rupestral vegetation

4.4.6.1 (*Festuca rubra*) – [*Hieracium pilosella*] grassland

4.4.6.2 [*Trifolium arvense*] – [*Hieracium pilosella*] grassland

4.4.6.3 [*Hieracium pilosella*] – [*Trifolium arvense*] rockland

4.4.6.4 [*Festuca novae-zelandiae*] – [*Coprosma propinqua*] rockland

4.4.7 Rupestral vegetation on Marlborough limestone

[*Pachystegia insignis*] – [*Elymus solandri*] rockland

- a Type with *Poa cita*
- b Type with *Coprosma propinqua*

Appendix 3

Climatic Ranges of Carmichaelia

Introduction

Climatic ranges of species, assessed in relation to their current distribution, are the product of the potential of these species to persist under certain climatic conditions in interaction with a wide range of abiotic and biotic factors, such as geology, soil type, or competition, that further influence the distribution of the species (Barbour et al. 1987). An understanding of the climatic ranges of species, therefore, provides insight into some of the factors determining their distribution.

The South Island *Carmichaelia* species vary widely in their geographical distribution. While some are considered local endemics of relatively small areas (e.g., *C. astonii, C. hollowayi*), others occur widely over large parts of the country (e.g., *C. australis, C. kirkii*; see section 3.3). The differences in the geographical ranges of the species are likely to be associated with differences in their climatic ranges, in particular, as the climatic conditions in the South Island of New Zealand vary considerably between the various regions (see section 2.3).

Based on their present distribution, this chapter analyses the current climatic ranges of the ten *Carmichaelia* species introduced in section 3.3, with the aim of identifying the main climatic factors influencing their distribution in the South Island of New Zealand and to gain a better understanding of their current status.

Methods

The analysis included the sites of all presently known populations of the ten *Carmichaelia* species, based on field visits during the past three years, information provided by the Department of Conservation, and records in the herbaria at WELT, AK, and CHR. Herbaria specimens were interpreted as representing current populations, if they were collected after 1970, and later surveys had not shown their extinction (Table 1; Appendix 1). *C. australis* was only included with locations in the north and east of the South Island, as this represented the main study area.

For all sites, climate data were obtained from Landcare Research, New Zealand (J. Leathwick, Landcare Research, pers. comm.). These data are derived based on the geographical coordinates and elevation of each site. Climatic variables are estimated using climate surfaces developed as thin-plate splines which are fitted to average monthly climate data from meteorological stations throughout the country (Leathwick 2001; Leathwick and Whitehead 2001).

Table 1: *Carmichaelia* species and number of localities included in the analysis.

Species	**Number of sites included**
C. astonii	5
C. australis	64
C. crassicaule	43
C. curta	10
C. hollowayi	3
C. juncea	4
C. kirkii	25
C. muritai	1
C. stevensonii	6
C. vexillata	22
All 10 species	183

The following climatic variables were used:

T_a - Mean annual temperature,

T_W - Seasonality of temperature regime,

$$\left[\left(\frac{J-\overline{J}}{\sigma_J}\right)-\left(\frac{T-\overline{T}}{\sigma_T}\right)\right]*\sigma_J \ ,$$

where J = July minimum temperature, T = mean annual temperature,

$\overline{J}$ = mean of J, σ_J = standard deviation of J, etc. (see Leathwick 2001),

Sol_a - Mean annual solar radiation,

Sol_W - Seasonality of solar radiation regime,

$$\left[\left(\frac{J-\overline{J}}{\sigma_J}\right)-\left(\frac{S-\overline{S}}{\sigma_S}\right)\right]*\sigma_J \ ,$$

where J = June solar radiation, S = annual solar radiation,

$\overline{J}$ = mean of J, σ_J = standard deviation of J, etc. (see Leathwick 2001),

P_a - Mean annual precipitation,

VPD_M - Mean vapour pressure deficit at 0900 h in March.

These variables were chosen, as they correlate strongly with the distribution of New Zealand tree species, and are thought to be major drivers of New Zealand vegetation patterns in general (Leathwick 2001; Leathwick and Whitehead 2001). Seasonality of temperature and solar radiation regimes express the levels of these variables in winter relative to their annual means.

To gain an understanding of the climatic conditions associated with the occurrence of the *Carmichaelia* species, I analysed the ranges and means each species showed for each climatic variable, as well as the relationships between the species considering two or all variables at the same time. The latter was achieved using canonical discriminant analysis (SAS Version 8.01, SAS Institute Inc.).

Results

The *Carmichaelia* species varied considerably in the climatic means associated with their current distribution, but their climatic ranges for the individual variables overlapped to a large extent (Fig. 1). Mean annual temperatures ranged from 5 - 13°C over all species, with *C. muritai* showing the highest (12.5°C) and *C. crassicaule* the lowest (7.6 ± 0.17°C) average. Temperature seasonality was particularly pronounced for *C. curta*, reflecting comparatively cold winter temperatures at the sites of this species. *C. astonii*, *C. muritai*, and *C. stevensonii*, in contrast, were subject to relatively warm winter temperatures. These three species were further conspicuous for high levels of mean annual solar radiation. *C. hollowayi* and *C. juncea* showed the lowest means for this variable, but the range for sites of *C. juncea* was wide. Contrasting the low annual mean, habitats of *C. juncea* showed comparatively high levels of solar radiation in winter, while the other species occurred at sites with little seasonality for this variable.

Mean annual precipitation clearly distinguished the sites of *C. juncea* from those of the other species. *C. juncea* was recorded from sites with a rainfall range from just below 2000 to 5000 mm/a, while all other species occurred in areas with upper rainfall limits below or just above 2000 mm, and minima as low as 420 mm/a (*C. vexillata*). Corresponding with the high precipitation, sites of *C. juncea* showed the lowest values of March vapour pressure deficit (0.22 ±0.05 kPa). Most species were subject to means around 0.4 kPa, with sites of *C. astonii* showing the highest deficits (0.58 ± 0.04 kPa).

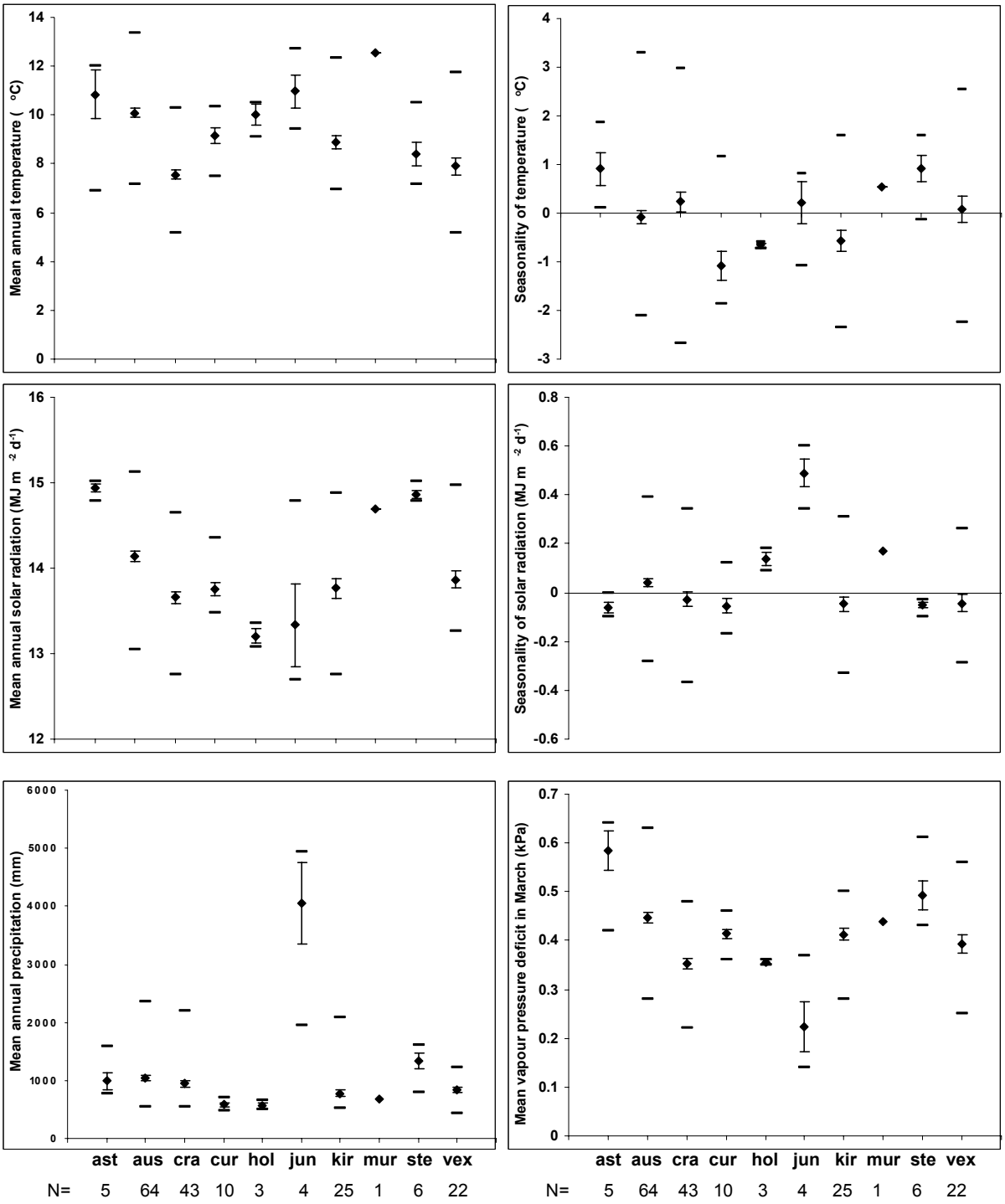

Fig. 1: Means (± 1 SE) of climatic variables and upper and lower limits associated with the presently known sites of the study species. (ast - *Carmichaelia astonii*, aus - *C. australis* , cra - *C. crassicaule*, cur - *C. curta*, hol - *C. hollowayi*, jun - *C. juncea*, kir - *C. kirkii*, mur - *C. muritai*, ste - *C. stevensonii*, vex - *C. vexillata*).

Several species were notable for their small ranges for some or all of the climatic variables. They were species for which only few, geographically close locations were known. Particularly, *C. hollowayi* showed little variation in the climatic characteristics of its three sites. *C. astonii* and *C. stevensonii* occurred in locations with constantly high annual means of solar radiation, and little seasonality for this factor. Locations of *C. curta* were

characterised by a particularly narrow range of annual precipitation (480-712 mm/a). *C. muritai* was only included with one of the two known locations. However, as the second population is located in similar coastal habitat only 9 km further north, the climatic variables are unlikely to vary much from the data used.

C. juncea was excluded from all following analyses, as, due to the very high annual precipitation levels, its locations were climatically so distinct, that they dominated the analyses and obscured patterns among the other species.

When mean annual temperature and precipitation were considered simultaneously, *C. australis* separated from *C. crassicaule*, *C. vexillata*, *C. curta*, and *C. hollowayi* (Fig. 2). Most locations of *C. australis* were characterised by either higher temperatures or higher precipitation than found at the sites of the other species. In addition, *C. crassicaule*, *C. vexillata*, *C. curta*, and *C. hollowayi* showed a trend of decreasing precipitation in their habitats with increasing mean annual temperature. *C. kirkii*, *C. stevensonii*, *C. astonii* and *C. muritai* showed stronger overlap with the climatic range of *C. australis*.

The relationship of mean annual precipitation and vapour pressure deficit in March showed a stronger overlap of the climatic ranges of the species (Fig. 3). At a given level of annual precipitation, *C. astonii*, *C. stevensonii*, and *C. australis* usually occurred at sites with higher vapour pressure deficits than the other species. *C. crassicaule* and *C. kirkii* showed their upper limit at around 0.5 kPa, while the range of *C. vexillata* extended to 0.56 kPa. The locations of *C. hollowayi* and *C. curta* showed similar ranges of annual precipitation, but vapour pressure deficits were higher at *C. curta* sites. The *C. muritai* site grouped close to those of *C. curta*, with a mean annual precipitation of 668 mm and a vapour pressure deficit of 0.44 kPa.

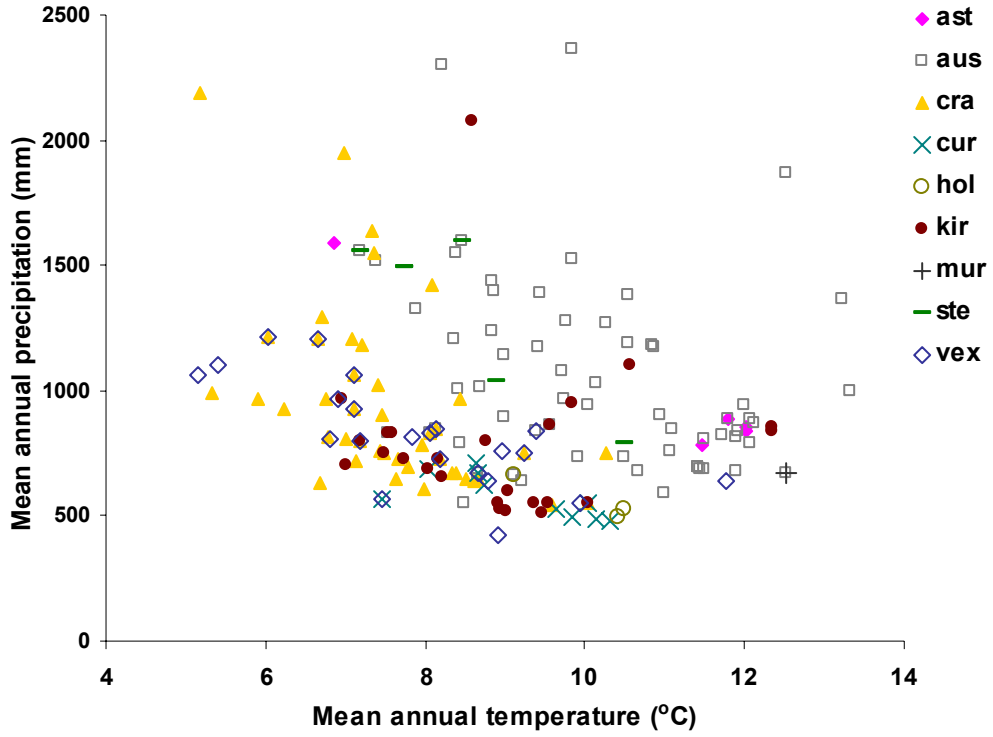

Fig. 2: Distribution of *Carmichaelia* species relative to mean annual temperature and precipitation.

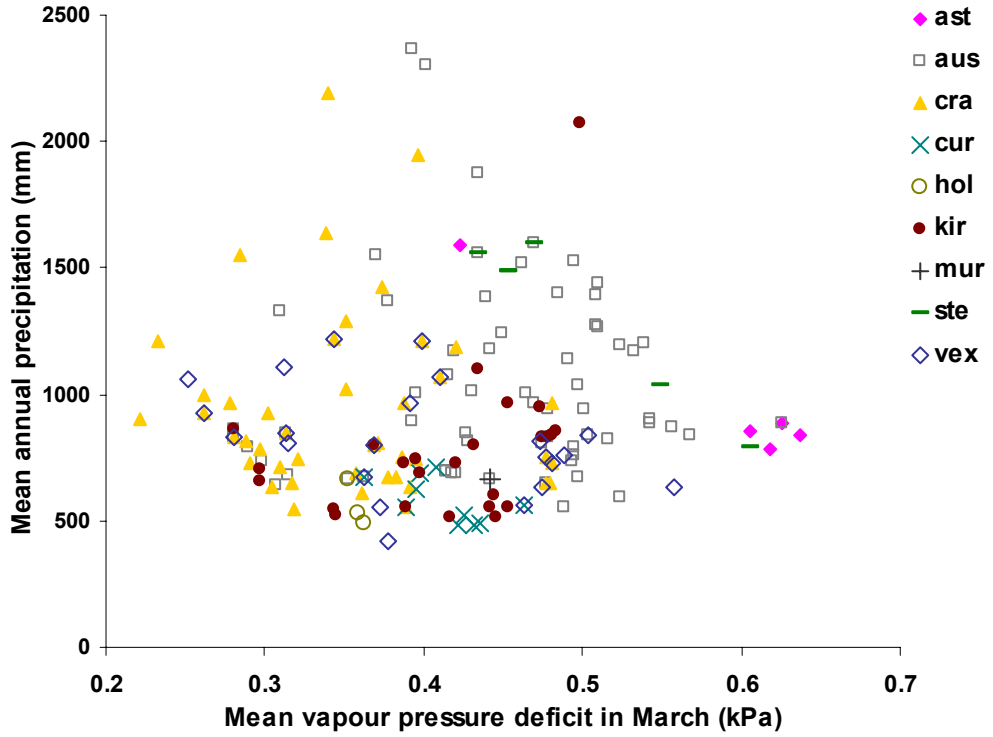

Fig. 3: Distribution of *Carmichaelia* species relative to mean vapour pressure deficit in March and annual precipitation.

The canonical discriminant analysis including all six climatic variables showed a similar separation of the species (Fig. 4). The first canonical variable (Can 1) accounted for 65% of the variation (eigenvalue 1.12) and was mainly determined by mean annual temperature and the vapour pressure deficit in March (Table 2). *C. astonii*, *C. muritai*, *C. stevensonii*, and *C. australis* showed relatively high values and separated along this axis from the other species, with *C. kirkii* showing the strongest overlap.

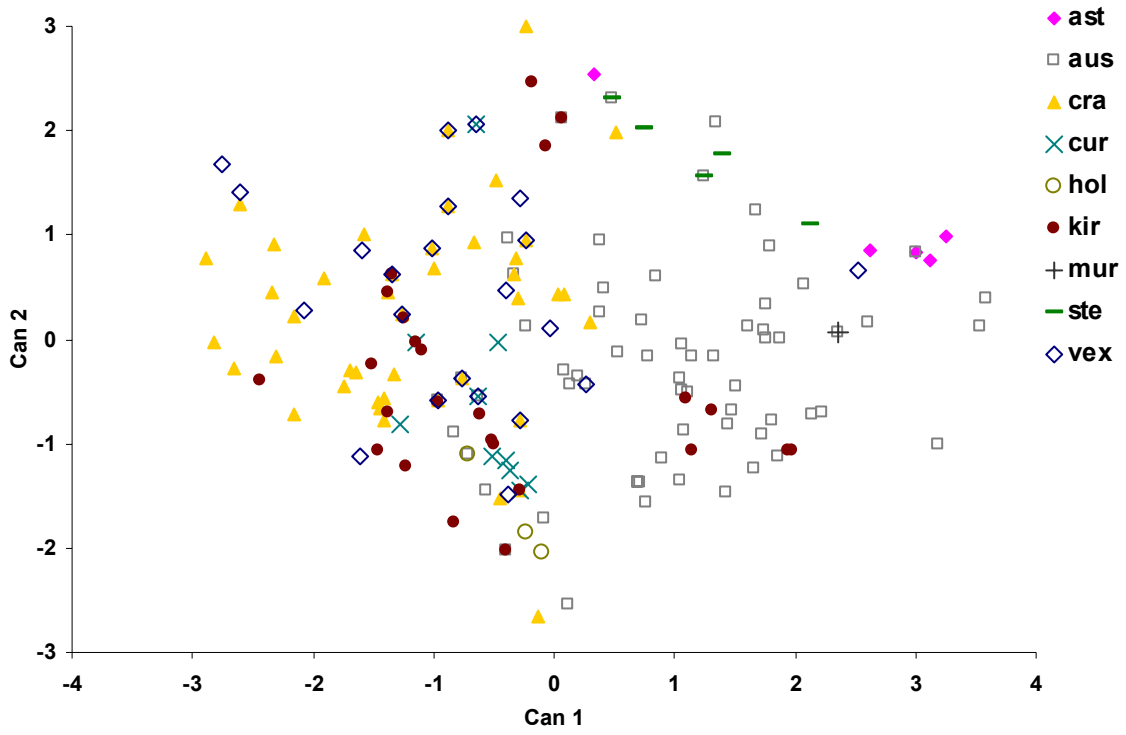

Fig. 4: Distribution of *Carmichaelia* species relative to the first two canonical variables based on the climatic characteristics of their present sites (species as in Fig. 1).

Table 2: Total-sample standardised coefficients and explanatory power of the first three canonical variables (Can 1-3) from the canonical discriminant analysis of climate variables associated with present locations of the *Carmichaelia* species.

Variable	Can 1	Can 2	Can 3
T_a	0.753	-0.678	0.689
T_W	0.156	0.545	-0.076
Sol_a	0.278	0.851	0.336
Sol_W	0.405	-0.112	-0.305
P_a	0.326	-0.224	0.916
VPD_M	0.588	-0.005	-1.365
Variation explained	65%	18%	9%

The second canonical variable (Can 2) was distinctly weaker in its capacity to spread the species (eigenvalue 0.31), and explained only 18% of variation. The main separating factors were annual solar radiation and seasonality of temperatures in interaction with mean annual temperatures. *C. crassicaule*, *C. kirkii*, *C. vexillata*, and *C. australis* were represented by locations spreading over the whole range of this variable, while *C. astonii* and *C. stevensonii* ranged at the upper end and *C. curta* and *C. hollowayi* at the lower.

The third canonical variable was not considered further, as it was comparatively weak (eigenvalue 0.16) and explained only 9% of variation.

Based on their means for all six canonical variables calculated in the analysis, *C. kirkii*, *C. curta, C. crassicaule* and *C. vexillata* were the closest species in the canonical space (Table 3). *C. crassicaule* and *C. muritai* were the most distant, the latter being relatively distant to all study species, including *C. astonii* and *C. stevensonii*. *C. australis*, in contrast, was relatively close to all species, except for *C. muritai*. *C. hollowayi* was closest to *C. kirkii* and *C. curta*, and most distant to *C. astonii* and *C. muritai*.

Table 3: Generalised squared distances between the species.

Species	ast	aus	cra	cur	hol	kir	mur	ste	vex
ast	0								
aus	6.67	0							
cra	16.68	5.01	0						
cur	13.91	3.88	2.46	0					
hol	17.53	4.89	5.33	2.86	0				
kir	12.03	2.51	1.44	0.56	2.79	0			
mur	18.61	15.98	25.95	22.04	24.32	23.66	0		
ste	5.17	4.48	8.13	9.58	15.75	7.61	19.28	0	
vex	12.66	4.14	0.64	1.47	5.20	0.95	23.43	6.05	0

The *a posteriori* assignment of the location data to the different species showed high percentages of correct allocations for the species that were only represented by few populations (Table 4). *C. astonii*, *C. curta*, *C. hollowayi*, *C. muritai*, and *C. stevensonii* were represented by a maximum of ten locations each and the *a posteriori* classification was 70-100% correct. Although this could indicate that the climatic ranges of these species were well defined and distinct from those of the other species, it was more likely to be an artefact caused by the small number of locations used in the analysis.

The other species showed correct allocations for 4 - 51% of their locations indicating relatively large climatic ranges. *C. kirkii* was the most extreme case having only one location correctly identified. The other sites were grouped to all other species except *C. astonii* and *C. muritai,* the two most distant species to *C. kirkii* with respect to species means. The same

was the case for sites of *C. crassicaule*, although the rate of correct allocations was higher. *C. vexillata* sites were mainly wrongly assigned to *C. crassicaule* and *C. curta*, whose species means were closest. However, one of its sites was allocated to the relatively distant *C. astonii*. *C. australis* locations were spread over all species.

Table 4: *A posteriori* classification of the site specific climate data to the *Carmichaelia* species; absolute numbers are given above percentages for each species.

Species	ast	aus	cra	cur	hol	kir	mur	ste	vex	Total
ast	4	0	0	0	0	0	0	1	0	5
	80	0	0	0	0	0	0	20	0	100
aus	3	31	1	4	7	4	4	8	2	64
	5	48	2	6	11	6	6	13	3	100
cra	0	2	22	5	4	1	0	2	7	43
	0	5	51	12	9	2	0	5	16	100
cur	0	0	0	7	1	0	0	0	2	10
	0	0	0	70	10	0	0	0	20	100
hol	0	0	0	0	3	0	0	0	0	3
	0	0	0	0	100	0	0	0	0	100
kir	0	5	2	5	5	1	0	3	4	25
	0	20	8	20	20	4	0	12	16	100
mur	0	0	0	0	0	0	1	0	0	1
	0	0	0	0	0	0	100	0	0	100
ste	1	0	0	0	0	0	0	5	0	6
	17	0	0	0	0	0	0	83	0	100
vex	1	0	7	6	2	0	0	0	6	22
	5	0	32	27	9	0	0	0	27	100
Total	9	38	32	27	22	6	5	19	21	179
	5	21	18	15	12	3	3	11	12	100

Overall, the analysis separated five groups of *Carmichaelia* species characterised by similar climatic ranges. High levels of mean annual precipitation at its sites clearly separated *C. juncea* from all other species. *C. astonii*, *C. muritai* and *C. stevensonii* formed a group characterised by relatively high levels for both canonical variables in the discriminant analysis (Fig. 4). However, variation within this group was relatively high; in particular, *C. muritai* was relatively distant to *C. astonii* and *C. stevensonii* (Table 3). *C. crassicaule*, *C. curta*, *C. hollowayi*, *C. kirkii*, and *C. vexillata* were all characterised by relatively low values for the first canonical variable, and their overall means showed relatively small distances in the canonical space. However, as the species differed clearly in the extent of their ranges they were separated into two groups. *C. crassicaule*, *C. kirkii*, and *C. vexillata* were characterised by wide climatic ranges, while the ranges of *C. curta* and *C. hollowayi* were relatively narrow (Fig. 4, Table 4). *C. australis* was separated from all other species by occupying an intermediary position between the groups.

Discussion

Grouping of Species

The grouping of the *Carmichaelia* species in relation to their climatic ranges corresponded clearly with their geographical ranges. The sharp west-east contrast in mean annual precipitation, typical for the climate of the South Island of New Zealand (Coulter 1975), separated the West Coast species *C. juncea* from all other species. *C. astonii*, *C. muritai*, and *C. stevensonii* were grouped together because of their high values for both canonical variables in the discriminant analysis. All three species are restricted to the Marlborough area characterised by a generally warmer climate and higher mean annual solar radiation compared to other regions in the South Island (Coulter 1975). *C. crassicaule*, *C. kirkii*, and *C. vexillata* were characterised by wide climatic ranges with low values for the first canonical variable. Accordingly, they are widespread species occurring along the east of the South Island, with strongholds in cooler, southern areas. The narrow climatic ranges of *C. curta* and *C. hollowayi* corresponded with their narrow geographical ranges. Both species are restricted to areas in southern Canterbury and northern Otago. *C. australis* is the most widespread *Carmichaelia* species, with populations in the east and west of the South Island, ranging from coastal sites in the NW Nelson area south to a latitude of about 45°. Furthermore, *C. australis* is the only study species with current populations in the North Island of New Zealand (Heenan 1996). Accordingly, *C. australis* was characterised by a very wide climatic range. As the distribution data used in the analysis included only *C. australis* populations in the north and east of the South Island, its range was intermediate between the Marlborough and the 'southern' species. The true climatic range of *C. australis* is likely to be much wider.

Current Ranges as Products of Human Impact

The present geographical and climatic ranges of the *Carmichaelia* species are not necessarily the ones the species occupied prior to human settlement. Changes in the environment caused by direct and indirect human impact have changed the geographical distribution of plant species in New Zealand (Wardle 1991), and with this most likely also their climatic ranges. The two *Carmichaelia* species *C. juncea* and *C. curta*, for example, used to be more widespread, with both their ranges extending further to the east than today (Fig. 3.14, Fig. 3.20 in section 3.3). Other species, such as the grassland species *C. crassicaule* and *C. vexillata*, in contrast, may have expanded their ranges since the beginning of human settlement, as the overall grassland area increased with progressing land clearance (Mc Glone 2001). Human interference, therefore, represents an additional factor, influencing the distribution of species in today's environment.

Current Ranges as Products of Plant Physiological Processes

The main climatic factors differentiating the various *Carmichaelia* species were mean annual temperature, mean vapour pressure deficit in March, mean annual solar radiation, and temperature seasonality. Similar relationships have been found in a number of other studies. For example, Leathwick (1995) found that mean annual temperature and annual solar radiation are the strongest correlates determining the distribution of New Zealand forest trees. Shao and Halpin (1995), Stephenson (1998), and Leathwick and Whitehead (2001) showed that variables expressing water deficits have a strong impact on the distribution of plant species. The fact that these results were in agreement with the findings presented here indicated that, despite the changes caused by human impact, the current climatic ranges of the *Carmichaelia* species still reflected ranges determined by plant physiological processes. The results, therefore, give indications for climatic factors influencing the distribution of the species, as well as for adaptations of the species towards the various variables.

Adaptation to Water Stress

The strong influence of vapour pressure deficit on the separation of the *Carmichaelia* species was somewhat surprising, as they are generally very drought tolerant plants (Heenan 1997). The importance of the vapour pressure deficit, therefore, indicated differences in the drought tolerance of the species. This was further supported by the distribution of the species relative to March vapour pressure deficit and mean annual precipitation (Fig. 3), as these two factors together reflected the degree of water stress plants are subject to at a site. In particular, *C. astonii*, *C. stevensonii*, *C. australis,* and *C. vexillata* were recorded from sites with distinctly higher levels of water stress than the other species. For *C. astonii* and *C. vexillata*, this tolerance to water stress was supported by their relatively good performance under the impact of root competition observed in chapter 5. However the findings in the competition study did not confirm such tolerance for *C. stevensonii* and *C. australis*.

The climate data used in the analysis did not consider extreme climatic events, although these are relatively common in most areas of New Zealand and likely to have an impact on the distribution of plants (Bannister 1986; Leathwick & Whitehead 2001). In particular, the east of the South Island frequently experiences strong warm winds and periods of drought (Coulter 1975). Although *Carmichaelia* are generally well adapted to drought conditions (Heenan 1997), their tolerance to extreme events could vary between species and further influence their distribution.

Evaluation of Current Status

The extent of the current climatic or geographical ranges of species does not allow drawing inferences on the need of species for conservation management. The results of this study illustrated that narrow ranges do not necessarily indicate threat, and wide ranges do not necessarily imply that species are safe. To correctly evaluate the current status of species, their current ranges have to be considered in view of their history. Here, a benchmark is needed, to which the current distribution of species can be compared. Ideally, this benchmark would reflect the situation prior to human influence, but records of the pre-human, and in fact, pre-European distribution of species in New Zealand do usually not exist. The benchmark, therefore, has to be formed by the earliest records available, accepting the limitation that this does most likely not reflect the original distribution of the species.

West Coast Species

C. juncea

The current climatic range of *C. juncea* reflected the climatic conditions of the West Coast of the South Island of New Zealand, where all present populations of *C. juncea* occur. The climate is characterised by high rainfall averages, low vapour pressure deficits, warm annual temperatures, and relatively high levels of solar radiation during the usually clearer winter months (Coulter 1975; Brenstrum 1999).

However, historic records collected for *C. juncea* show that this species used to be more widespread in the past, and that the current distribution is the result of an extensive range contraction due to the extinction of populations. *C. juncea* has been reported from Fiordland, Central Otago, Canterbury, and southern Marlborough (see Fig. 3.20), as well as from one site in the North Island (Hawkes Bay). As these areas are characterised by very different climate regimes compared to the West Coast (chapter 2.3), the current climatic range of *C. juncea* is likely to merely represent a subset of its original range. The factors behind the decline of the species are likely to be human-induced changes in habitat conditions, in particular, the introduction of mammalian herbivores (see chapter 6).

Marlborough Species

C. astonii, *C. muritai*, and *C. stevensonii* currently occur at sites that are characterised by relatively warm winter temperatures and high levels of annual solar radiation, the latter being a distinctive feature of the climate of the Marlborough region (Coulter 1975). With respect to

the other climatic variables, the three species varied considerably. In particular, *C. muritai* appeared separate from the other two.

C. astonii

C. astonii occurs in the coastal hill country of southern Marlborough, mainly in areas where Amuri limestone emerges as base rock material. The climatic range of *C. astonii* was relatively narrow, with the exception of an outlier population at George Pass (Seaward Kaikoura Ranges).

Only a few historic records exist for *C. astonii*, but all report the species from the same areas where it is found today, indicating that it is naturally range restricted. *C. astonii* is associated with a number of species considered to be local endemics for the southern Marlborough region (e.g., *Pachystegia insignis*, *Heliohebe hulkeana*, see section 4.4.7). Furthermore, local endemism is a common phenomenon amongst rupestral species in New Zealand, in particular, in limestone habitats (Wardle 1991; Molloy 1994; Molloy et al. 1999). While the climatic range of *C. astonii* is likely to always have been relatively narrow, its distribution is probably mainly determined by the availability of suitable limestone substrate.

C. muritai

C. muritai is only known from two sites in southern Marlborough, growing on coastal cliffs of conglomerate above the beach. Only one location was used in the analysis. However, as the second site is located in similar coastal habitat, only 9 km to the north, the climatic variables are unlikely to vary much from the data used. The conditions were characterised by high mean annual temperatures and comparatively high levels of winter solar radiation. Wood anatomical features characterise *C. muritai* as less adapted to drought conditions than *C. stevensonii* (Heenan 1997). Consistent with this, the relationship between mean annual precipitation and March vapour pressure deficit suggested that the plants are subject to lower levels of water stress than *C. astonii* and *C. stevensonii* at their sites.

C. muritai has only recently been recognised as separate species within *Carmichaelia* (Purdie 1985). As no historical records exist, it is unknown whether this species used to be more widespread.

C. stevensonii

C. stevensonii is presently restricted to relatively high altitudes (600-1100 m a.s.l.) in the Inland and Seaward Kaikoura Ranges. The climatic conditions at its sites showed relatively large variation for all variables except the constantly high annual solar radiation typical for all Marlborough sites, and a low seasonality for this factor. Due to the higher altitudes, mean

annual temperatures were slightly lower than for the other Marlborough species, while precipitation was higher at most sites.

Historical records describe *C. stevensonii* from several lowland locations, indicating that the climatic range of this species used to be wider than it is today. The extinction of *C. stevensonii* at these lowland sites could be the result of changes in climatic conditions, but seem more likely to have been caused by competition with invasive plants and use of the land for grazing. Furthermore, it is uncertain whether these lowland sites ever supported intact, self-sustaining populations, or whether the records stem from vagrant plants that occasionally established from seeds dispersed from higher altitudes (P. Heenan, Landcare Research, pers. comm.).

Widespread 'Southern' Species

The widespread 'southern' species, *C. crassicaule*, *C. kirkii*, and *C. vexillata* are characterised by wide geographical ranges extending from Marlborough south to Otago, but all three species show their stronghold in the southern areas (Fig. 3.11, Fig. 3.23, Fig. 3.31). The climatic ranges of these species were also wide, illustrating that they are adapted to a wide range of climatic conditions.

C. crassicaule

The current distribution of *C. crassicaule* is not very well understood. As this species occurs widespread and scattered in many, usually small populations, it has received little attention in population surveys. Historic records do not indicate range contraction, but it is unknown whether current populations are stable or in decline. A general lack of recruitment observed during this study as well as the extinction of at least one historic population point towards a decline of *C. crassicaule*, and anthropogenic impacts, in particular herbivory, are likely to be the causes for this.

C. kirkii

The locations of *C. kirkii* grouped into three clusters in the canonical space of the discriminant analysis (Fig. 4). Each cluster represented a distinct area along the east of the South Island, characterised by distinct climatic conditions. The Marlborough sites of *C. kirkii* were characterised by the high levels of annual solar radiation typical for this region. Mean annual temperatures were relatively low (7.0-7.6°C) due to the high altitudes of the sites (960-1100 m a.s.l.). In contrast, temperatures were comparatively high at the sites in Mid Canterbury and at Banks Peninsula (8.6-12.3°C). Although most of the locations of *C. kirkii* were characterised by medium levels of annual precipitation (500-1100 mm), the species can

also occur under extremely high levels as indicated by one site with 2076 mm rainfall/a (Cox's Downs, Mt Cook Station).

The particularly wide climatic range of *C. kirkii* suggested that this species used to very be widespread throughout the eastern South Island. A number of historic records report the species from localities where it is now extinct (e.g., New Brighton (Christchurch), Lake Aviemore (Waitaki Valley), Otepopo River (North Otago)). Currently a number of extant populations, in particular, those at the edge of the geographical range are immediately threatened with extinction (e.g., Lynbrook, populations on Banks Peninsula), illustrating that this species is in decline due to habitat loss caused by human land use.

C. vexillata

The climatic range of *C. vexillata* showed strong overlap with that of *C. crassicaule*. Both species have a similar geographical distribution, and furthermore, occur in similar habitat types (chapter 4).

C. vexillata shows a characteristic disjunct distribution with most of its current populations in southern areas (Mackenzie Basin, Central Otago), and two populations in Marlborough. Disjunct distribution has been pointed out for a number of indigenous species in New Zealand, but the underlying causes are unclear (c.f. Wardle 1963; Burrows 1965, Mc Glone 1985).

As *C. vexillata* as a distinct species has only recently been segregated from *C. monroi*, its current distribution is not fully understood. Historic records describe the species from within its present geographic range, and a recent survey of historic populations in the Mackenzie Basin showed that most of these populations were still extant (Wardle 2000). This could indicate a stable status for this species, under the current environmental conditions.

<u>Range Restricted 'Southern' species</u>

The range restricted 'southern' species, *C. curta* and *C. hollowayi*, occur in the area of the Mackenzie Basin and upper Waitaki Valley in southern Canterbury. This area is characterised by a relatively continental climate. Temperatures show strong seasonality with particularly cold winters, and mean annual precipitation is low (< 712 mm/a in habitats of *C. curta* and *C. hollowayi*).

C. curta

Historic records describe a wider distribution of *C. curta* in the past, with collections made in the lower Waitaki Valley, coastal areas south of Oamaru, and Central Otago. This indicates that, although *C. curta* is adapted to the harsh conditions of its current sites, its original climatic range extended to more favourable areas. *C. curta* is likely to have been displaced from these sites to the very dry and infertile sites it occupies today, by competition with introduced plants and herbivory by introduced mammals (Wardle 1991; and see section 4.4.6).

C. hollowayi

The current geographical range of *C. hollowayi* stretches over a distance of only 30 km along the southern side of the Waitaki Valley. The only historical record extends its range into the adjacent hill country to the south (Mt St. Mary). Similar to *C. astonii*, *C. hollowayi* is a rupestral species of limestone habitats, and most likely naturally range restricted (c.f. Molloy et al. 1999). Its distribution is therefore likely to be largely dependent on availability of suitable substrate.

C. australis

The distribution of *C. australis* relative to mean annual precipitation and temperature showed that this species occurs in warmer areas with higher annual precipitation than the 'southern' *Carmichaelia* species. *C. australis* is not known from sites with annual mean temperatures below 7.2°C and annual precipitation below 550 mm. These climatic factors are likely to determine its southern distributional limit in the east of the South Island.

Historic records for *C. australis* are numerous, and confirm the geographic range for this species in its current extent. Although some of the recorded populations may have gone extinct, the species is still widespread and occurs over a wide range of habitat types. Furthermore, as *C. australis* seems to favour disturbed and modified sites (chapter 4), it is likely to benefit from human land management, and might therefore have extended its range in historical times. This is further supported by the occurrence of hybrids with several other *Carmichaelia* species (*C. hollowayi*, *C. juncea*, *C. monroi*, *C. nana*, *C. vexillata*; Heenan 1998; S. Courtney, DoC Nelson, pers. comm.).

Implications for Conservation Management

The results of this study could significantly contribute to the successful conservation management of *Carmichaelia* species, as the assessed climatic ranges could be used to approximate the potential distribution of the species (c.f. Shao & Halpin 1995; Leathwick 2001; Leathwick & Whitehead 2001). This would allow predictions on where further populations may occur, directing survey efforts, as well as the identification of suitable locations for restoration work.

However, a limitations arises from the fact that the climate data used in this study did not reflect microclimatic conditions in the habitats of *Carmichaelia* species. The data are derived from interpolation of climate data measured at irregularly, and relatively widely spaced meteorological stations (Leathwick & Whitehead 2001). Therefore, they reflect the general climate of an area, but not specific site conditions. This could introduce an error in the assessed climatic ranges of the *Carmichaelia* species. For example, the local conditions for plants on rock outcrop sites are likely to deviate from the general climate of an area, depending on prominence, aspect, and base rock material of the inhabited microsite. Such differences need to be considered when sites for the potential restoration of species are chosen. Chapter 4 provides detailed descriptions of the habitats of the various species that should be used in addition to the climatic variables.

References

Barbour, M. G., Burk, J. H. and Pitts, W. D. 1987. Terrestrial plant ecology. - Benjamin/Cummings Publishing Company, Menlo Park.

Brenstrum, E. 1999. The New Zealand weather book. - Craig Potton Publishing, Nelson.

Burrows, C. J. 1965. Some discontinuous distributions of plants within New Zealand and their ecological significance. Part II: disjunctions between Otago-Souuthland and Nelson-Marlborough and related distribution patterns. - Tuatara 13: 9-29.

Coulter, J. D. 1975. The climate. - In: Kuschel, G. (ed.) Biogeography and ecology in New Zealand. W. Junk, Den Haag, pp. 87-138.

Heenan, P. B. 1998. An emended circumscription of *Carmichaelia*, with new combinations, a key, and notes on hybrids. - New Zealand Journal of Botany 36: 53-63.

Leathwick, J. R. 1995. Climatic relationships of some New Zealand forest tree species. - Journal of Vegetation Science 6: 237-248.

Leathwick, J. R. 2001. New Zealand's potential forest pattern as predicted from current species-environment relationships. - New Zealand Journal of Botany 39: 447-464.

Leathwick, J. R. and Whitehead, D. 2001. Soil atmospheric water deficits and the distribution of New Zealand's indigenous tree species. - Functional Ecology 15: 233-242.

Mc Glone, M. S. 1985. Plant biogeography and the Cenozoic history of New Zealand. - New Zealand Journal of Botany 23: 723-749.

Mc Glone, M. S. 2001. The origin of the indigenous grasslands of southeastern South Island in relation to pre-human woody ecosystems. - New Zealand Journal of Ecology 25: 1-15.

Molloy, B. P. J. 1994. Observations on the ecology and conservation of *Australopyrum calcis* (Triticeae: Gramineae) in New Zealand. - New Zealand Journal of Botany 32: 37-51.

Molloy, B. P. J., Edgar, E., Heenan, P. B. and de Lange, P. J. 1999. New species of *Poa* (Gramineae) and *Ischnocarpus* (Brassicaceae) from limestone, North Otago, South Island, New Zealand. - New Zealand Journal of Botany 37: 41-50.

Shao, G. and Halpin, P. N. 1995. Climatic controls of eastern North American coastal tree and shrub distributions. - Journal of Biogeography 22: 1083-1089.

Stephenson, N. L. 1998. Actual evapotranspiration and deficit: biologically meaningful correlates of vegetation distribution across spatial scales. - Journal of Biogeography 25: 855-870.

Wardle, K. 2000. The conservation status of *Carmichaelia vexillata* in the Mackenzie Basin. - Internal report, Department of Conservation, Christchurch.

Wardle, P. 1963. Evolution and distribution of the New Zealand flora, as affected by Quaternary climates. - New Zealand Journal of Botany 1: 3-17.

Wardle, P. 1991. Vegetation of New Zealand. - Cambridge University Press, Cambridge.

Appendix 4

Effects of Shade Treatments on Microclimate in the Light Competition Experiment

Introduction

The shade frames used in the light competition experiment (see chapter 5) were expected to modify the microclimate in the shaded plots, as such effects have previously been observed in similar experiments (Grime & Jeffrey 1965; Augspurger 1984; Williams and Buxton 1989). Shade cloth shields incoming irradiance over the whole spectrum of light, including the longer wavelengths that create heat. Together with a slowing effect on air movement, this is likely to alter the temperature and relative humidity regime for plants placed under such a shade treatment (Grime & Jeffrey 1965; Augspurger 1984; Williams and Buxton 1989).

These effects of the shade frames introduced an additional source of variation into the experiment, that could not be separated from the actual effect of light competition. To quantify the direction and magnitude of the changes, temperature and relative humidity were monitored over a two day period during the experiment.

Methods

A Cambell CR 21 X datalogger with Cambell 207 temperature and relative humidity sensors was installed to monitor two replicates on opposite sides of the glasshouse over a two day period during the experiment (16/17 Dec 2000). The sensors were placed on plant level in the middle of each treatment plot. Measurements were saved every 30 minutes.

The lights in the glasshouse were turned on from 8 am to midnight every day. Temperature was set at a minimum of 17°C and fluctuated above this level depending on weather conditions. Relative humidity was not controlled.

A relative calibration of the sensors was performed with measurements under uniform conditions for all sensors.

Results

Temperature

During the night, the temperatures in the glasshouse reached the set minimum of 17 °C (Fig. 1). As soon as the lights were turned on in the morning, the glasshouse heated up, and temperatures reached maximum levels between 2 and 4 pm. Then a drop in temperature occurred followed by another increase in the early evening. When the lights were turned off at midnight, temperatures dropped quickly to cooler night levels.

Differences between the treatments were small during the night hours. The unshaded plots were slightly cooler than the shaded plots, with the largest difference being 1.4 °C (compared to the dark shade treatment). During the day, the open plots reached higher temperatures than the shaded plots. The largest difference occurred, when, on day 1, the unshaded plots heated up to 33.1 °C, while the medium shade treatment remained at 27.2 °C. The dark shade treatment effected slightly warmer temperatures than the medium shade treatment during the day as well as at night (max. difference 2.1 °C), except for a short period in the evening, when the medium shade treatment was up to 0.5 °C warmer.

The temperature differences in the treatment plots resulted in different daily amplitudes for the three treatments. In the open plots, daytime temperatures were up to 17 °C above night temperatures, while this difference was 10.3 °C and 11.1 °C for the medium and dark shade treatments, respectively.

Relative Humidity

The relative humidity in the experimental plots reached levels between 80 and 90% during the night, and decreased during the day corresponding to the rise in temperatures (Fig. 1). During the night the open and the dark shade plots were very similar in their humidity levels, while the medium shade treatment was up to 6.9% lower (compared to dark shade). During the day, humidity levels in the open plots were up to 15% lower than in the shaded plots, while differences between the medium and dark shade treatments were variable, but overall relatively small.

The daytime humidity levels in the open plots were up to 49% below the ones measured at night, while this amplitude for the shaded plots reached 36 and 37% for the medium and dark shade treatment, respectively.

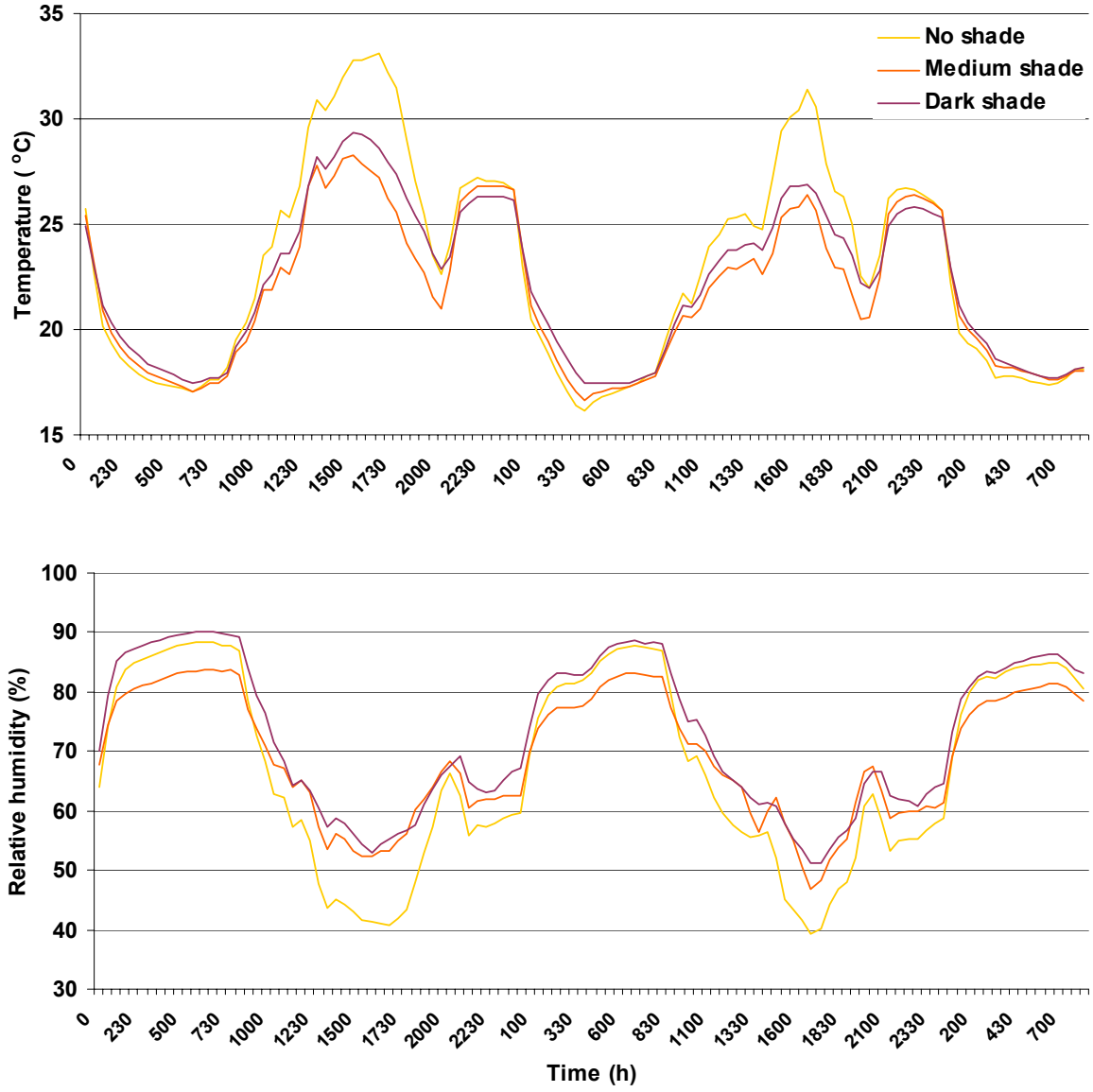

Fig. 1: Temperature and relative humidity regimes in the three shade treatments of the light competition experiment.

Discussion

The assessment of the microclimatic conditions in the three experimental treatments showed that the plants in the unshaded plots were subject to larger daily fluctuations in temperature and relative humidity. While the treatments showed similar levels of temperature and relative humidity at night, the sheltering effect of the shade frames became obvious during the day, when changes were buffered compared to the unshaded plots. Differences between the two shade treatments were relatively small contrasting the distinctly higher temperatures and lower humidity levels in the unshaded plots.

The slightly higher temperatures in the dark shade treatment compared to the medium treatment could have been caused by two factors: the black shade cloth could have absorbed more heat, or it could have stopped airflow more effectively than the lighter, green cloth used for the medium shade treatment. This latter mechanism could also have lead to the higher humidity levels observed in the dark treatment at night. The higher humidity in the 'no shade' treatments is likely to have resulted from the cooler night temperatures.

The abrupt drop in temperature in all treatments during the afternoon was probably caused by changes in the amount of direct sunlight falling into the glasshouse, as the sun moved temporarily behind parts of the glasshouse construction and adjacent trees. The fact that the temperature levels remained otherwise relatively high until the lights were turned off at midnight illustrated the relatively strong effect of the artificial lights on the temperature regime in the glasshouse.

The observed variations in microclimate associated with the shade treatments are likely to correspond with similar conditions in the field. Shady scrub and forest habitats are known to buffer climatic fluctuations (Walter 1973), and shady sites are generally associated with lower temperatures, higher relative humidity, and also higher soil moisture levels compared to adjacent sites in the open (Augspurger 1984; Popma and Bongers 1988). Higher soil moisture levels were noted in the shaded plots during the experiment, but this was not quantified, and the watering regime adapted accordingly.

References

Augspurger, C. K. 1984. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. - Journal of Ecology 72: 777-795.

Grime, J. P. and Jeffrey, D. W. 1965. Seedling establishment in vertical gradients of sunlight. - Journal of Ecology 53: 621-642.

Popma, J. and Bongers, F. 1988. The effects of canopy gaps on growth and morphology of seedlings of rain forest species. - Oecologia 75: 625-632.

Walter, H. 1973. Vegetation of the earth in relation to climate and the eco-physiological conditions. - Springer, London.

Williams, P. A. and Buxton, R. P. 1989. Response to reduced irradiance of 15 species of native and adventive shrub and tree seedlings from eastern Canterbury. - New Zealand Journal of Ecology 12: 95-101.

Appendix 5

Management Recommendations for Carmichaelia

This section discusses concrete management strategies for the conservation of the ten study species, based on the groups developed in chapter 7, but also considering the actual significance of threats in the current habitats of the individual species. While the grouping of the *Carmichaelia* species was based on their vulnerability to the impacts of introduced species and habitat loss, the following discussion also includes further threats to the species that have previously been suggested or were observed during the field work for this study.

Assessment of Current Status

A sound knowledge of the current status of rare species, i.e. their exact distribution and abundance is essential to accurately evaluate their conservation needs (c.f. Hogbin and Peakall 2000; Garcia et al. 2002). Over the last four years, the New Zealand Department of Conservation has conducted partial field surveys for most of the *Carmichaelia* species (*C. astonii*, *C. curta*, *C. juncea*, *C. kirkii*, *C. stevensonii*, *C. vexillata*), with the overall result that the species were more widespread and abundant than previously thought (Wardle, 1999, 2000a,b; Grove 2001; J. Clayton-Greenee, DoC Renwick, pers. comm.; P. Knightbridge, DoC Hokitika, pers. comm.). Even for two of the rarest species, *C. hollowayi* and *C. muritai*, additional populations have only recently been found (P. Heenan, Landcare Research, Lincoln, pers. comm.; J. Clayton-Greenee, DoC Renwick, pers. comm.). These positive results illustrate that the distribution and abundance of *Carmichaelia* species are not sufficiently known, highlighting the need for further survey work.

In addition, to fully understand the current status of the *Carmichaelia* species, we need to view their abundance and distribution before the background of the history of their habitats and past impacts. For example, the range of *C. curta* was believed to be restricted to the Waitaki Valley area in southern Canterbury (Heenan 1995). However, during the past four years, several new populations were found extending the range by 65 km further north. While this could simply be the result of more thorough survey work, it could also indicate a recovery of this species following the decline of rabbit populations. Rabbits had a devastating impact on the native vegetation in inland areas of New Zealand until the recent introduction of the RCD virus in 1997 (Norbury 2001; Clout 2002). Rabbit numbers have collapsed since, and

the vegetation has begun to recover. The prominence of small plants, with evident juvenile morphology in the *C. curta* population discovered at Mackenzie Pass in February 2001, suggested that this 'new' population was the result of such vegetation recovery.

Recruitment Failure

Recruitment failure has been recognised as a common problem among rare and threatened plants in New Zealand (Dopson et al. 1999), as well as other parts of the world (e.g., Zaafouri and Chaieb 1999; Auld and Denham 2001). Many *Carmichaelia* populations appeared to show symptoms of this, as they consist of adult plants of presumably even age, and at best a small number of very young juveniles, lacking the mixed-aged structure indicating successful recruitment. This was particularly striking in many populations of *C. crassicaule*, the three visited populations of *C. hollowayi*, the Seaview population of *C. muritai*, and for *C. stevensonii* at Mt Alexander.

Recruitment failure can be caused by a variety of reasons, affecting various stages in the reproductive cycle. A number of studies have observed severe reductions in seed set or the production of viable seed, as a consequence of habitat fragmentation and decreases in population size (e.g., Jennersten 1995; Giblin and Hamilton 1999; Matsumura and Washitani 2000). This did not seem to apply to the *Carmichaelia* species, as large numbers of viable seeds were found for most species during the three years of this study. The only exceptions were *C. hollowayi*, where seed set was sparse, and *C. stevensonii*, for which no seeds were found in the wild, but were abundant in cultivation. These species would need to be monitored over longer periods of time and in additional populations, to confirm the apparent lack of seed production. Chapter 6 illustrated that severe browse can lead to reduced seed production of *Carmichaelia* species, and subsequent recruitment failure. In some populations, in particular, those of *C. muritai*, *C. crassicaule*, and *C. curta*, intensive seed predation by native weevils was observed as a potential threat, but further research would have to clarify its significance.

Recruitment failure because of lack of seed germination can occur, if the current habitat conditions do not meet the germination requirements of a species. For example, the seeds of the rare New Zealand shrub *Hebe cupressoides* are adapted to germination under full light conditions. As invasive grasses create relatively shady conditions in the ground layer of most *H. cupressoides* habitats today, a large number of seeds fail to germinate (also Frost 1981; Widyatmoko and Norton 1997). *Carmichaelia* seeds have been shown to germinate readily in light as well as in darkness (Grüner and Heenan 2001), and juveniles of all species were

repeatedly observed in the field (except *C. muritai*). This suggests that the apparent lack of recruitment in *Carmichaelia* populations must be caused by factors affecting the plants at a later stage, during their development from juveniles to adults.

Vulnerability of Juveniles to Competition

The results of this study illustrated that competition with introduced plants is likely to play a major role in the inhibition of recruitment of the *Carmichaelia* species. In particular, root competition severely inhibited the productivity of seedlings and juveniles (chapter 5), indicating that this factor could limit the successful establishment of all *Carmichaelia* in the field. However, as levels of competition in the field are likely to vary and may not compare to the levels applied in the experiment, field trials would be needed to clarify this impact.

Vulnerability of Juveniles to Herbivory

The vulnerability to herbivory assessed in this study referred to the vulnerability of adults, and the probability that seed production was prevented by the impact. However, herbivory seemed likely to also pose a threat to the persistence of *Carmichaelia* species by affecting earlier life-stages. Moreover, while the vulnerability of adult *Carmichaelia* varied depending on their plant architecture, the repeated observation of browsed juveniles and young adults of all species (except *C. muritai*) in the field indicated that the impact of herbivory at these early life-stages is severe for all species. The conservation management of *Carmichaelia* species, therefore, should aim in particular, at protecting juveniles and young adults from the impact of mammalian herbivores. For the range restricted species and very localised populations, this could be achieved by fencing. On a larger scale, efficient animal control would be needed.

Bevill et al. (1999) found that the short-term protection of juveniles ensured the persistence of a population of Pitcher's thistle (*Cirsium pitcheri*), as adults of this species are less vulnerable to the impact. Similar, to their experience, short-term protection is likely to be sufficient for those *Carmichaelia* species whose adults are relatively tolerant to herbivory. The tall growing scrub and tree species would need to be protected until the plants reach a size at which they become less vulnerable to the impact of the herbivores. This threshold size is likely to depend on the size of the herbivores present (c.f. Belovsky 1997), and has been found to be around 100 cm in height for *C. crassicaule*, where cattle and sheep are present (G. Loh, DoC Dunedin, pers. comm.). As the dwarf shrub species (except

C. vexillata), and the low growing shrubs, e.g. *C. curta*, remain highly vulnerable as adults (chapter 6), populations of these species would need to be protected at all life stages.

Conservation Management in Modified Environments

The management strategies discussed below focus on the conservation of the *Carmichaelia* species in their current habitats. These habitats are not necessarily the ones the species evolved in, or where they occurred before the arrival of humans in New Zealand. As direct and indirect anthropogenic impacts have since modified all regions and habitat types in this country, *Carmichaelia* species occur today in either highly modified remnants of their original habitats, in induced communities that have developed since human settlement, or in refuge sites to which the species retreated in escape from changes in the environment. Trying to preserve native species in such modified and induced habitats represents in some ways a minimalistic approach, and usually requires ongoing management. However, restoration of the original habitats is in most cases impossible, as their characteristics are not known, and furthermore, inflicted changes to the environment, such as the invasion of introduced species, are usually irreversible. Nevertheless, besides concentrating on populations of threatened species and their persistence, conservation management should also pursue species recovery on larger scales, aiming at coming as close as possible to the restoration of typical New Zealand habitats and landscapes, with self-sustaining populations of native species (c.f. Given 1994; Huxel and Hastings 1999).

Research by Management

Wherever possible, management should be implemented in the form of experiments, comprising treatments and control (Caughley 1994). Where this is not feasible, regular monitoring assessing changes in the population trends of the threatened species and in the intensity of threats needs to be implemented (Campbell et al. 2002). Such a ‘research by management’ approach maximises the effectiveness of conservation management, as it allows for the control of success as well as for adaptive management, when mistakes become apparent or conditions change (Hodgson 1991; Bowles and Whelan 1994; Simberloff 1999; Possingham et al. 2001).

Group 1: *C. astonii* and *C. hollowayi*

The rock outcrop species, *C. astonii* and *C. hollowayi* were characterised by high vulnerability to shoot competition, herbivory and habitat loss, but relatively low vulnerability to root competition. Conservation management, therefore, would have to mainly consider the first three factors.

C. astonii

Threats

Although *C. astonii* was identified as being vulnerable to shoot competition, this impact is unlikely to pose an immediate threat in the current habitats of this species, as invasion by adventives, in particular, tall growing plants, is naturally limited. The characteristically steep rock faces, without topsoil or accumulation of fine rock material, represent relatively unfavourable habitat for most invaders.

The steepness of the habitat is also likely to pose a barrier to the impact of introduced mammalian herbivores, as many plants are not accessible for them. Accordingly, only limited browse damage, on relatively accessible plants was observed on *C. astonii* at Ward, although the area is used for grazing of sheep and cattle. In the second population visited (Isolated Creek), no browse damage was noted during this study, but has been reported in the past from there, and other inland populations (S. Courtney, DoC Nelson, pers. comm.).

Habitat loss seems to mainly affect the persistence of the *C. astonii* population at Ward, as this area is used to quarry limestone.

Conservation Management

The conservation management of *C. astonii* should aim at keeping herbivore control in the areas the populations occur in at current levels. This means the grazing intensity at Ward should not be increased, and control of feral mammals at the inland locations needs to be continued. This approach should be complimented by regular monitoring of browse damage on the plants, to ensure the adequacy of the management. At Ward, a management plan for the quarry area should be discussed with the land owner.

C. hollowayi

Threats

In contrast to *C. astonii*, *C. hollowayi* occurs in flatter terrain with a higher level of invasion by adventive species (section 4.4.6.1). In particular, introduced grasses form relatively dense swards, causing increased competitive conditions.

The flatter terrain also makes *C. hollowayi* plants more accessible to mammalian herbivores, such as livestock, rabbits, rats (Molloy et al. 1999), and possibly possums. While only limited fresh browse damage was observed during the study, most plants showed signs of very severe previous damage, indicating intermittent occurrence of severe browse impact.

Habitat modification and destruction also seem to pose a more imminent threat to *C. hollowayi* than to *C. astonii*. Three of the four known populations of *C. hollowayi* are located on farmland, being subject to livestock grazing and fertiliser application. The fourth population is located inside a cultural heritage area retired from farm management, but represents also the smallest population with only two adults.

An additional threat to the persistence of *C. hollowayi* arises from the fact that it forms fertile hybrids with the associated *C. australis* (Heenan 1998). Hybridisation poses a serious threat to rare species, as genetic extinction can occur in less than five generations (Wolf et al. 2001). As *C. hollowayi* are probably relatively long-lived plants, this process is likely to be slow. However, the currently present '*C. hollowayi* ' vary remarkably in their morphology, already suggesting an element of hybridisation within the population.

Conservation Management

The conservation management of *C. hollowayi* needs to limit the levels of competition in the habitats of this species. As populations are very localised, this could be achieved by manual weed control. An experimental weeding programme has already been implemented at one of the sites (Awahokomo; N. Head, DoC Christchurch, pers. comm.) and should be continued. In addition, strict herbivore control should be a priority for conservation management at all sites of *C. hollowayi*. To avert further habitat modification or destruction, all currently known sites of *C. hollowayi* should be put under legal protection. One of the sites has the status of a voluntary covenant under the Queen Elisabeth II National Trust (Awahokomo), and tighter rules for its management should be negotiated. Genetic studies would be needed to clarify the current status of the species in relation to *C. australis*.

Group 2: *C. muritai, C. stevensonii, C. kirkii*

C. muritai, *C. stevensonii*, and *C. kirkii* formed a group of species with relatively low vulnerability to shoot competition and herbivory, but high vulnerability to the impact of root competition and habitat loss. The limitation of the latter two should, therefore, receive priority in the conservation management of these species.

All three species occur in relatively dense scrub vegetation with naturally limited levels of root competition in the ground layer. The aim of conservation management should be to preserve or restore such habitats. Depending on the context of a site, restoration could be achieved by either facilitating natural regeneration or by planting of shrubs naturally associated with the *Carmichaelia* species (for species lists see chapter 4). Often, the presence of mammalian herbivores poses a problem, as they break into stands of scrub and open them up for invasion by light-demanding, adventive plants (Fox and Fox 1986). However, when these herbivores are removed, by fencing or animal control, a further increase of invasion by adventive plants may occur (see section 7.4). These changes needs to be carefully monitored, and if necessary, mitigated.

All three species might have originally occurred in more open sites. In particular, *C. muritai* and *C. stevensonii* seem adapted to relatively unstable and disturbed sites with relatively open vegetation. However, in the current environment, especially with the current high levels of invasion, it would be difficult to maintain populations in open habitats without on-going intensive management. The competition experiment showed that these species are able to regenerate in limited light. Creating dense scrub habitat therefore, seems to provide an option to retain or re-create self-sustaining populations of these species under the current conditions.

C. muritai

Threats

The levels of invasion by adventive species in the habitats of *C. muritai* varied between the two sites currently known for this species. At Seaview, the vegetation was dominated by introduced grasses, except on the steepest slopes and in bouldery gullies. Establishment sites *for C. muritai* seedlings appeared limited, and while Williams et al. (1996) reported some regeneration, none was observed during the two summers of 1999/2000 and 2000/2001. The second population is located at a site where introduced plants have invaded

to a lesser degree, and abundant regeneration of *C. muritai* is present (J. Clayton-Greenee, DoC Renwick, pers. comm.).

The Seaview population is fenced against larger herbivores such as goats or chamois, while the site at White Bluff is freely accessible, although parts of it are very steep. Only one incidence of browse was observed during this study, when a possum had bitten off a branch in the crown of one of the trees at Seaview.

Habitat loss seems to be an immediate threat to *C. muritai*, in particular, when considering the extreme rarity of the species, together with the natural instability of the habitat.

Conservation Management

The *C. muritai* population at Seaview is located in a Scientific Reserve, established by the Department of Conservation. This population has been subject to relatively intensive conservation management (J. Clayton-Greenee, DoC Renwick, pers. comm.). The site was cleared from overgrowing boxthorn (*Lycium ferocissimum*), and restoration plantings were undertaken to restore the original coastal shrubland. The *C. muritai* population was surveyed, and then monitored over time. Plants were propagated from seed, and the off-spring planted at the site. In summer 1999/2000, an establishment trial was set up, including a weeding treatment to assess the effect of competition on regeneration. All these conservation actions should be continued. Based on the results of the establishment trial, further weeding in the population should be undertaken.

The *C. muritai* site at White Bluffs is in Maori ownership, with restricted access to the public. The presence of *C. muritai* at this site was officially only discovered in late 2001. A detailed survey is needed to assess size and structure of the population. The habitat at White Bluffs appeared less modified than that at Seaview. However, although local and in low numbers, aggressive adventive grasses were present (*Nassella trichotoma, Bromus diandrus*). These need to be removed before further spread occurs.

The extreme rarity of *C. muritai* calls for ex-situ conservation efforts, preserving this species in case the current habitats are destroyed by catastrophic events. Storage of seeds as an emergency reserve could be an option. However, it needs to be considered that seeds lose their viability over time. Only 5% of *C. muritai* seeds were found to be viable after 17 years of open storage (Grüner and Heenan 2001). Populations could be established in cultivation, or in the form of artificial populations in the wild. The latter has already been undertaken at Marfells Beach, about 15 km south of the Seaview site (J. Clayton-Greenee, pers. comm.).

Additional sites could be selected, based on the characteristics of the current habitats and plant communities described in chapter 4.

C. stevensonii

Threats

The levels of invasion in the habitats of *C. stevensonii* depended on the density of the shrubland habitat. Where stands were opened up, e.g., at Mt Alexander, introduced grasses were dominant in the ground layer (chapter 4).

Severe browse damage by ungulates was observed on juveniles and young adults of *C. stevensonii*.

Habitat loss and modification represent further threats to *C. stevensonii*. Persistent grazing pressure could destroy remnants of relatively dense shrubland currently providing habitat for *C. stevensonii*. Furthermore, the habitats of *C. stevensonii* are naturally unstable, which poses a threat to the species, considering its current rarity.

Conservation Management

The scrub communities typically associated with *C. stevensonii* need to be maintained or restored. Where they are in relatively remote areas with sufficient seed source from adjacent areas, this can probably be achieved by natural regeneration, if herbivores, in particular, ungulates (feral and domestic) in the areas are controlled. In more modified areas, restoration planting, in combination with animal control and removal of weeds, need to be considered.

C. kirkii

Threats

Similar to *C. stevensonii*, the levels of invasion in habitats of *C. kirkii* depended on the density of the existing shrubland. Most of the extant populations of *C. kirkii* are located on land used for grazing, and the scrub has been opened up by grazing animals and fire. Invaders are mainly exotic grasses, increasing the levels of competition in the ground layer.

Very little direct browse was observed on *C. kirkii*. The plants are likely to be relatively well protected inside the divaricate, often prickly shrubs they grow in.

Habitat loss and modification also threaten the persistence of *C. kirkii*, as scrub is still being cleared for farming or other land development.

Dopson et al. (1999) mention careless weed-spraying as a further threat to the species.

Conservation Management

C. kirkii appeared not as vulnerable to the impact of root competition as the other scrub species *C. muritai* and *C. stevensonii* (chapter 5). However, the presented results assessed only the relative vulnerability of the species, leaving the actual effect of competition on the plants to be tested in the field. Until this is done, using the precautionary principle, conservation management of *C. kirkii* should also aim at limiting root competition in the habitats of this species. The typical 'grey scrub' habitat needs to be maintained or restored by applying the same principles as discussed above for *C. stevensonii*. The *C. kirkii* populations at the distributional limit of this species seem to be particularly threatened, and should receive priority in the conservation management of this species to maintain the genetic potential of this species.

Group 3: *C. curta, and C. juncea*

C. curta, and *C. juncea* were similar in being highly vulnerable to shoot competition and herbivory, and showing intermediate vulnerability to root competition and habitat loss. This vulnerability profile characterised these species as the most vulnerable among the *Carmichaelia* species. The conservation management of these species needs to consider all four factors, although in particular, the effects of shoot competition and herbivory.

C. curta

Threats

Similar to *C. crassicaule*, many of the extant populations of *C. curta* seem to occur at sites, where the plants can at least partly escape the impact of introduced species. The rock outcrops and highly depleted grassland vegetation that served as habitats for C. curta usually showed low levels of invasion by adventives. However, invasion by European broom (*Cytisus scoparius*) and pine (*Pinus contorta*) were observed at two sites (Awahokomo, Deep Stream).

Livestock and to a lesser degree, hares seemed to be the main mammalian herbivores feeding on *C. curta*. The intensity of the damage varied between sites depending on

management and accessibility. Tall plants were only found on land not used for grazing or inaccessible to the herbivores, such as roadsides and rock outcrops.

Habitat loss and modification threatening *C. curta* are mainly caused by farm management (Grove 2001).

Dopson et al. (1999) suggest over-collecting and careless weed-spraying, in particular in the roadside habitats, as further threats to *C. curta*.

Conservation Management

The conservation management of *C. curta* needs to control shrub invasion in the current habitats to limit the impact of shoot competition. Where populations are located on farmland, release from grazing could be implemented. However, the possibility of a subsequent increase in competition levels needs to be considered, monitored, and if necessary mitigated. Habitat loss could be partly averted by legal protection of selected populations. Increased information to the public, and collaboration with Transit New Zealand on protection of the species could reduce the threats of over-collecting and weed-spraying.

C. juncea

Threats

The levels of invasion by adventives varied strongly in the habitats of *C. juncea*. While competition did not appear to pose a problem on the recent alluvial surfaces forming the habitat of *C. juncea* in the lowland populations of South Westland, exotic grasses were relatively prominent in the upland populations at Welcome Flat. The steep rock outcrop habitat in NW Nelson showed low levels of invasion.

Herbivory also varied strongly between sites. Here, the lowland populations in South Westland were most severely affected, in particular, the plants in the Waiho River, where hares browsed the plants to ground level. The populations at Welcome Flat and in NW Nelson did not suffer any browse damage during the study period, but plants at Welcome Flat showed signs of previous damage, probably caused by chamois (c.f. Yockney and Hickling 2000).

Habitat loss caused by natural catastrophes or human impact seems to present a further threat to *C. juncea*, at least when considering its current rarity (Norton et al. 1998). The natural habitat of this species is very dynamic, with loss of local populations being an integral

part. However these dynamics are not very well understood, and the status of *C. juncea* in the Waiho River indicates, that the balance of maintaining self-sustaining populations in these systems might be disrupted. The upper limit of the population in the Waiho River has moved about 5 km downstream since the 1970s (c.f. Wardle 1975), and the current levels of herbivory are likely to have a serious impact on the populations dynamics by preventing seed production (chapter 6).

As *C. juncea* forms fertile hybrids with *C. australis* as well as *C. arborea*, its persistence is further threatened by genetic introgression. Hybrids with *C. australis* are common in NW Nelson, and a large number of *C. arborea* hybrids have been observed in South Westland, in particular, at Welcome Flat.

Conservation Management

In the lowland populations of *C. juncea* in South Westland, hare control should receive highest priority. Unfortunately, efficient hare control methods have not yet been developed (Wong and Hickling 1999), although this should be of high priority for conservation in New Zealand in general, as a detrimental impact of hares on native vegetation is increasingly noted throughout the country (e.g., Flux 1967; Horne 1979; Blay 1989; Wong and Hickling 1999; Norbury 2001).

At Welcome Flat, herbivore control at the current level seems sufficient. However, monitoring of herbivore damage on the *C. juncea* plants should be implemented to control the continued adequacy of this management. The *C. juncea* population at Welcome Flat is already part of a monitoring programme conducted by the Department of Conservation to assess growth and survival of adult plants. To gain a better understanding of the impact of competition and herbivory at this site, this monitoring should be extended to the establishment of seedlings and young adults, ideally in the form of an experimental study.

The conservation management of *C. juncea* in South Westland is likely to further benefit from a better understanding of the population dynamics of this species. In South Westland, *C. juncea* occurs in highly dynamic riverbed habitats. The populations in these rivers can be characterised as typical meta-populations, consisting of distinct sub-populations on separate riverbed islands or parts of the river terrace system (Watkinson 1986). Extinction and re-colonisation of sites are integral parts of the natural dynamics of such meta-populations, and their functioning needs to be understood to enable their successful conservation management (Gilpin 1987; Mc Eachern et al. 1994; Simberloff 1998; Johst et al. 2002).

The protection of the last extant population of *C. juncea* in NW Nelson should be of high priority in the conservation management of *C. juncea*, as its protection is likely to also protect the genetic diversity within the species. The main threat at this site appears to be habitat loss and destruction, and measures, such as restriction of access, should be considered to avert this.

Ex-situ propagation should be considered as a further management strategy for *C. juncea*, as the species is only known from four extant populations, and the immediacy of the extinction risk is largely unclear, due to the lack of understanding regarding the population dynamics of this species. However, care needs to be taken, that only true *C. juncea* are chosen for propagation, as previous attempts have resulted in the establishment of hybrid populations (S. Courtney, DoC Nelson, pers. comm.; pers. obs.).

Currently attempts are being made by the Department of Conservation at restoring some of the previous geographical range of *C. juncea*. Plant material from two extinct populations has been re-discovered in collections, and is being used to first establish ex-situ populations that could then be planted into the wild. The exact sites for these re-establishment projects could be selected based on descriptions in historical records, as well as on the habitat descriptions provided in this study.

Single species

C. crassicaule

C. crassicaule was distinct in its vulnerability profile, taking an intermediary position between *C. curta* and *C. juncea*, and *C. vexillata*. It was characterised by high vulnerability to herbivory, intermediate vulnerability to both mechanisms of competition, and low vulnerability to habitat loss. Conservation management should focus on the impact of herbivory, but also consider the impact of competition in the habitats of *C. crassicaule*.

Threats

Most *C. crassicaule* populations currently occur on land which is, or has been until recently, used for grazing. Levels of invasion by adventive plants are usually high, the main invaders being exotic grasses and forbs increasing the levels of root competition (chapter 4).

During this study, severe browse by livestock, hares, and rabbits was frequently observed. Often, the plants were browsed almost to ground level. An exception to this were populations

of *C. crassicaule* in rock outcrop habitat, where levels of plant invasion and herbivory damage were low. These sites are likely to represent refuges from the impacts of introduced species (c.f. Wardle 1991).

Conservation Management

Over the last ten years, substantial areas of the South Island high country have been retired from farm management as a result of tenure review. This is could potentially lead to a recovery of *C. crassicaule*, as grazing levels are reduced. However, the removal of livestock could also lead to an increase in invasion by adventives, the resulting higher competition levels averting the benefits of reduced herbivory (see section 7.4). A number of exclosure trials indicate that the removal of herbivores is generally beneficial for *C. crassicaule* (G. Loh, DoC Dunedin, pers. comm.; N. Ledgard, Forest Research, pers. comm.). Nevertheless, changes in the structure and composition of the associated vegetation after removal of herbivores should be carefully monitored. Such monitoring could, furthermore, clarify the significance of feral mammals such as rabbits and hares as threats to the persistence of *C. crassicaule*.

As *C. crassicaule* is a widespread species occurring in many scattered but usually small populations, it has so far received little attention in conservation. To gain a better understanding of its ecology and status selected populations throughout its range should be put under intensive conservation management, including research. This would also ensure the future persistence of this species throughout its range.

C. vexillata

Its vulnerability profile characterised *C. vexillata* as the least vulnerable species among the *Carmichaelia* studied. It showed low vulnerability to root competition, herbivory, and habitat loss, and intermediate vulnerability to shoot competition.

Threats

Levels of invasion in the habitats of *C. vexillata* were usually found to be high. However, as the invaders are mainly low growing grasses and forbs, they impose little shoot competition. Scrub reversion or spread of pines on retired grassland could pose a long-term threat to the species in some areas of the South Island.

Severe browse damage caused by livestock, rabbits, and hares was frequently observed.

Habitat loss and modification could pose a threat to *C. vexillata*, with the 'amelioration' of land for farm management or other development.

The vulnerability profile of *C. vexillata* could explain its current status and distribution. The species occurs relatively widespread in degraded grassland areas of the eastern South Island. These areas were grazed or subject to severe rabbit browse over extended periods of time. This means, they were kept open, with low levels of shoot competition. As *C. vexillata* is relatively tolerant to root competition, increasing invasion by adventive grasses and forbs did not pose an immediate threat. Similarly, browse by introduced herbivores was tolerated, allowing *C. vexillata* to persist.

Conservation Management

The conservation management of *C. vexillata* should aim at preventing invasion of taller growing plants into the habitats of this species. Where retired grasslands are reverting to tall tussock grasslands (c.f. Walker 2000) the status of *C. vexillata* needs to be monitored, and if necessary appropriate disturbance regimes implemented.

Although the species seemed relatively tolerant to herbivory, this impact should be controlled at least in selected populations of this species throughout its range, to allow for full development of plants. Monitoring of such populations might allow further insight into the ecology of this species, and its vulnerability to threats.

C. australis

C. australis also separated from all other species, being similar to the scrub species in its low vulnerability to herbivory and high vulnerability to root competition. However, it was distinct from these species due to a higher vulnerability to shoot competition, and lower vulnerability to habitat loss.

Threats

Levels of invasion in *C. australis* habitats were usually high, except where the species occurred on rock outcrops.

Browse damage varied with the accessibility of the plants. In open grassland areas, the damage was usually severe, with the plants being browsed to almost ground level. Frequently, larger plants were found growing inside other shrubs, such as matagouri

(*Discaria toumatou*) or small-leaved *Coprosma* species, that provided some protection from herbivores.

The habitats of *C. australis* were often relatively modified areas such as intensive grazing land, pine plantations, or roadsides. Habitat loss or modification, therefore, did not seem to pose threat to this species.

Conservation Management

C. australis is not considered in need of conservation management, as it occurs widespread and abundant. However, the study showed that it is not more tolerant or adapted to the impact of introduced species than the other *Carmichaelia*. Its ecological variability is likely to present an advantage to this species. Furthermore, *C. australis* seemed to prefer relatively mesic sites, and to benefit from disturbance, similar as it is known for matagouri (Wardle 1991). This indicated that the species might be better adapted than the other *Carmichaelia* species to the conditions and disturbance regimes created by human land management.

References

Auld, T. D. and Denham, A. J. 2001. Flora conservation issues at Kinchega National Park, western NSW. - Cunninghamia 7: 27-41.

Belovsky, G. E. 1997. Optimal foraging and community structure: The allometry of herbivore food selection and competition. - Evolutionary Ecology 11: 641-672.

Bevill, R. L., Louda, S. M. and Stanforth, L. M. 1999. Protection from natural enemies in managing rare plant species. - Conservation Biology 13: 1323-1331.

Blay, G., J. 1989. Food preferences of the European hare (*Lepus europaeus* Pallas) on a fescue grassland. - MSc thesis, University of Canterbury, Christchurch.

Bowles, M. L. and Whelan, C. J. 1994. Restoration of endangered species. Conceptual issues, planning and implementation. - Cambridge University Press, Cambridge.

Campbell, S. P., Clark, J. A., Crampton, L. H., Guerry, A. D., Hatch, L. T., Hosseini, P. R., Lawler, J. J. and O'Connor, R. J. 2002. An assessment of monitoring afforts in endangered species recovery plans. - Ecological Applications 12: 674-681.

Caughley, G. 1994. Directions in conservation biology. - Journal of Animal Ecology 63: 215-244.

Clout, M. N. 2002. Ecological and economic costs of alien vertebrates in New Zealand. - In: Pimentel, D. (ed.) Biological invasions. Economic and environmental costs of alien plant, animal, and microbe species. CRC Press, London, pp. 185-193.

Dopson, S. R., de Lange, P. J., Ogle, C. C., Rance, B. D., Courtney, S. P. and Molloy, J. 1999. The conservation requirements of New Zealand's nationally threatened vascular plants. - Threatened Species Occasional Publication 13, Department of Conservation, Wellington.

Flux, J. E. C. 1967. Hare numbers and diet in an alpine basin in New Zealand. - Proceedings of the New Zealand Ecological Society 14: 27-33.

Fox, M. D. and Fox, B. J. 1986. The susceptibility of natural communities to invasion. - In: Groves, R. H. and Burdon, J. J. (eds.) Ecology of biological invasions. Cambridge University Press, Cambridge.

Frost, L. C. 1981. The study of *Ranunculus ophioglossifolius* and its successful conservation at the Badgeworth Nature Reserve. - In: Synge, H. (ed.) The biological aspects of rare plant conservation. Wiley & Sons, Chichester, pp. 481-489.

Garcia, M. B., Guzman, D. and Goni, D. 2002. An evaluation of the status of five threatened plant species in the Pyrenees. - Biological Conservation 103: 151-161.

Giblin, D. E. and Hamilton, C. W. 1999. The relationship of reproductive biology to the rarity of endemic Aster curtus (Asteraceae). - Canadian Journal of Botany-Revue Canadienne De Botanique 77: 140-149.

Gilpin, M. E. 1987. Spatial structure and population vulnerability. - In: Soulé, M. E. (ed.) Viable populations for conservation. Cambridge University Press, Cambridge, pp. 125-139.

Given, D. R. 1994. Principles and practice of plant conservation. - Timber Press, Oregon.

Grove, P. 2001. The status of *Carmichaelia curta* in the Waitaki River catchment. - Canterbury Botanical Society Journal 35: 37-42.

Grüner, I. and Heenan, P. B. 2001. Viability and germination of seeds of *Carmichaelia* (Fabaceae) after prolonged storage. - New Zealand Journal of Botany 39: 125-131.

Heenan, P. B. 1995. A taxonomic revision of *Carmichaelia* (Fabaceae-Galegae) in New Zealand (part I). - New Zealand Journal of Botany 33: 455-475.

Heenan, P. B. 1998. An emended circumscription of *Carmichaelia*, with new combinations, a key, and notes on hybrids. - New Zealand Journal of Botany 36: 53-63.

Hodgson, J. G. 1991. Management for the conservation of plants with particular reference to the British flora. - In: Spellerberg, I. F., Goldsmith, F. B. and Morris, M. G. (eds.) The scientific management of temperate communities for conservation. Blackwell Science, Oxford, pp. 81-102.

Hogbin, P. M. and Peakall, R. 2000. The effective management of threatened flora: Lessons from the case of. - Pacific Conservation Biology 6: 238-244.

Horne, R. S. C. 1979. Seasonal and altitudinal variations in diet and abundance of the European hare (*Lepus europaeus* Pallas) in Tongariro National Park, New Zealand. - MSc thesis, Massey University, Palmerston North.

Huxel, G. R. and Hastings, A. 1999. Habitat loss, fragmentation, and restoration. - Restoration Ecology 7: 309-315.

Jennersten, O. 1995. Pollination in *Dianthus deltoides* (Caryophyllaceae): effects of habitat fragmentation on visitation and seed set. - In: Ehrenfeld, D. (ed.) Plant conservation. Readings from Conservation Biology. Society for Conservation Biology, Blackwell Science, Oxford, pp. 130-137.

Jesson, L., Kelly, D. and Sparrow, A. 2000. The importance of dispersal, disturbance, and competition for exotic plant invasions in Arthur's Pass National Park, New Zealand. - New Zealand Journal of Botany 38: 451-468.

Johst, K., Brandl, R. and Eber, S. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. - Oikos 98: 263-270.

Matsumura, C. and Washitani, I. 2000. Effects of population size and pollinator limitation on seed-set of *Primula sieboldii* populations in a fragmented landscape. - Ecological Research 15: 307-322.

Mc Eachern, A. K., Bowles, M. L. and Pavlovic, N. B. 1994. A metapopulation approach to Pitcher's thistle (*Cirsium pitcheri*) recovery in southern Lake Michigan dunes. - In: Bowles, M. L. and Whelan, C. J. (eds.) Restoration of endangered species. Conceptual issues, planning and implementation. Cambridge University Press, Cambridge, pp. 194-218.

Molloy, B. P. J., Edgar, E., Heenan, P. B. and de Lange, P. J. 1999. New species of *Poa* (Gramineae) and *Ischnocarpus* (Brassicaceae) from limestone, North Otago, South Island, New Zealand. - New Zealand Journal of Botany 37: 41-50.

Norbury, G. 2001. Advances in New Zealand mammalogy 1990-2000: lagomorphs. - Journal of the Royal Society of New Zealand 31: 83-97.

Norton, D. A., de Lange, P. J. and Miller, C. 1998. *Carmichaelia juncea* - a little known plant on the brink of extinction. - New Zealand Botanical Society Newsletter 52: 11-13.

Possingham, H. P., Andelman, S. J., Noon, B. R., Trombulak, S. and Pulliam, H. R. 2001. Making smart conservation decisions. - In: Soulé, M. E. and Orians, G. H. (eds.) Conservation Biology. Research priorities for the next decade. Island Press, Washington, pp. 225-244.

Simberloff, D. 1998. Small and declining populations. - In: Sutherland, W. J. (ed.) Conservation science and action. Blackwell Science, London, pp. 116-134.

Simberloff, D. 1999. The role of science in the preservation of forest biodiversity. - Forest Ecology and Management 115: 101-111.

Spira, T. P. 2001. Plant-pollinator interactions: A threatened mutualism with implications for the ecology and management of rare plants. - Natural Areas Journal 21: 78-88.

Walker, S. 2000. Post-pastoral changes in composition and guilds in a semi-arid conservation area, Central Otago, New Zealand. - New Zealand Journal of Ecology 24: 123-137.

Wardle, P. 1975. Vascular plants of Westland National Park (New Zealand) and neighbouring lowland and coastal areas. - New Zealand Journal of Botany 13: 497-545.

Wardle, P. 1991. Vegetation of New Zealand. - Cambridge University Press, Cambridge.

Watkinson, A. R. 1986. Plant population dynamics. - In: Crawley, M. J. (ed.) Plant ecology. Backwell Scientific Publications, Oxford, pp. 137-184.

Widyatmoko, D. and Norton, D. A. 1997. Conservation of the threatened shrub *Hebe cupressoides* (Scrophulariaceae), eastern South Island, New Zealand. - Biological Conservation 82: 193-201.

Williams, P. A., Norton, D. A. and Nicholas, J. M. 1996. Germination and seedling growth of an endangered native broom, *Chordospartium muritai* A.W. Purdie (Fabaceae), found in Marlborough, South Island, New Zealand. - New Zealand Journal of Botany 34: 199-204.

Wolf, D. E., Takebayashi, N. and Rieseberg, L. H. 2001. Predicting the risk of extinction through hybridization. - Conservation Biology 15: 1039-1053.

Wong, V. and Hickling, G. J. 1999. Assessment and management of hare impact on high-altitude vegetation. - Science for Conservation 116, Department of Conservation, Wellington.

Yockney, I. J. and Hickling, G. J. 2000. Distribution and diet of chamois (*Rupicapra rupicapra*) in Westland forests, South Island, New Zealand. - New Zealand Journal of Ecology 24: 31-38.

Zaafouri, M. S. and Chaieb, M. 1999. Threatened trees and shrubs of the southern Tunisia. - Acta Botanica Gallica 146: 361-373.

Appendix 6

The following paper was published in the New Zealand Journal of Botany 39 (2001), pp. 125-131. It was written in collaboration with my associate supervisor Dr. Peter Heenan, but is product of the first year of my PhD research, focusing on the ecology of *Carmichaelia*.